Testing the Cultural Intelligence Hypothesis in Orangutans:

Variation in Novelty Response, Exploration and Intelligence

Dissertation

zur

Erlangung der naturwissenschaftlichen Doktorwürde

(Dr. sc. nat.)

vorgelegt der

Matemathisch-naturwissenschaftlichen Fakultät

der Universität Zürich

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Zürich, 2016

"*Creativity is intelligence having fun*"

- Albert Einstein

Thesis summary

Culture is a key element in human evolution and one of the driving forces to greater intelligence. The capacity to attend to and learn necessary skills provided by our socio-cultural environment has been highly selected for and is a fundamental component of human nature. Nevertheless culture is not unique to humans. Accumulating evidence for culture in non-human animals has altered the question toward how cultural processes link to cognition and the evolution of intelligence: i.e. cultural intelligence. The principle behind *the Cultural Intelligence Hypothesis* is that increased opportunities to learn skills socially during development improve an individual's intellectual abilities. In species where such opportunities are abundant and frequent, it can be assumed that this makes it possible for selection to act upon underlying cognitive mechanisms and consequently promote intelligence on an evolutionary time scale. The core of my work is to apply *the Cultural Intelligence Hypotheses* to one of our closest living relatives, the orangutans (*Pongo spp*) and thereby feature the shared evolutionary history of cultural processes shaping intelligence.

Like in humans, culture in animals represents behavioral traditions founded on innovations, as the units of diversification. Thus, understanding the process of innovativeness is crucial in order to explain culture. It is commonly assumed that innovations arise in response to novelty, and therefore that innovative species are attracted to new things. Orangutan cultural diversity result from behavioral innovations, yet little is known about how orangutans respond to novelty. In my first study (*chapter 2*), I examined reactions toward novelty in wild orangutans through a set of field experiments. Results demonstrated strong conservatism, in form of passive avoidance of novelty. Although this outcome was expected based on previous experience with orangutans, it demonstrated that the intuitive link between innovativeness and a positive response to novelty does not hold for orangutans. I could show that they do not touch unfamiliar objects and thus are naturally not drawn to novelty and yet extensively explore familiar items within their habitats. These contradictive findings only make sense in the light of cultural intelligence: the pathway through which individuals integrate novel innovations is not by exploration of novel items, but rather due to social learning, which may include individual exploration of familiar items. In order to investigate the environmental influences of captivity, the same novel items were then presented to zoo-housed orangutans. Beyond the risk-free existence of a captive habitat, orangutans brought up in zoos experience increased social contact with conspecifics and social contact also with human caretakers, which is lacking in their natural habitat. In contrast to their wild conspecifics, all zoo individuals took an instant interest in the novel objects.

Inspired by the contrasting results on novelty response in captive and wild orangutans, I conducted an extensive review of the literature where I examine variation in neophobia in a broad comparative framework (*chapter 3*). In the review I predict that species with slow-paced life history, such as the

great apes, benefit from conservativeness in their natural habitats, because they can rely mainly on social learning rather than independent exploration. Interestingly, in captivity, trust in humans as role models erodes their innate neophobia, and even makes them rather neophilic due to their strong exploration tendency. The innovation paradox can thus be understood by considering a species dependence on role models, i.e. social learning, which is critically supportive of *the Cultural Intelligence Hypothesis*.

In my fourth chapter I examine the outcomes of a strong adaptation for social learning and focus on actually empirically testing *the Cultural Intelligence Hypothesis*. Since cultural species develop their skill set through social learning, selection on learning mechanisms must have been high. Consequently, species with systematically richer social environment may over time evolve to become more intelligent, reflected by larger brain size. To test this evolutionary perspective of *the Cultural Intelligence Hypothesis* was the primary goal of chapter 4. Over an evolutionary time scale, the two orangutan species, *Pongo abelii* and *Pongo pygmaeus*, have experienced different socio-ecological environments, reflected in higher social tolerance and greater sociability in Sumatran *P. abelii*. This in turn has favored transmission of skills resulting in larger skill pool and thus more frequent opportunities for social learning in *Pongo abelii*. In order to control for the variation in social- and ecological factors of the natural habitat, I performed a zoo study to compare cognitive abilities between the two *Pongo* species. The homogenous environments provided by zoos allowed me to detect any intrinsic differences between the two species. The findings illustrate the ultimate product of cultural intelligence and suggest a clear intrinsic difference in how the two *Pongo* species apply their learning ability, with *Pongo abelii* showing better problem solving skills. Not only did I find a species difference in cognitive performance but *P.abelii* also showed higher levels of inhibition and different styles of exploration. I conclude that this species difference in learning ability is consistent with a history of greater sociability and social tolerance in *Pongo abelii*.

My last chapter returns to how a captive life influences cognitive abilities and focuses on causes to inter-individual variation of problem-solving abilities. In collaboration with my colleague Laura Damerius we measured novelty response, exploration and cognitive performance in a large sample of captive housed orangutans from both zoos and rehabilitation stations. Our sample consisted of individuals varying in rearing conditions and duration of human exposure, which both are predicted to strongly alter an individual's cognitive performance. To estimate variation in reactions to humans among individuals with different rearing backgrounds, which we expected to be at least partly responsible for the variation in cognitive performance, we developed human orientation indices (*HOI-index*). Our results revealed that none of the other factors, such as the time in captivity, zoo versus sanctuary housing, species, age or rearing conditions influenced cognitive performance in any way. Instead, the social element of human attentiveness, i.e. the outcome of the HOI- test, was the strongest predictor of explorative behaviors leading to higher cognitive performance. In favor of *the Cultural*

Intelligence Hypothesis individuals that exhibit a high HOI exhibit a different attention structure and may have experienced a different nature of learning opportunities by attentiveness to humans. Thus, as humans become additional trusted role models for apes housed in captive environments their influence does not only wear down neophobia, as stated in chapter 2 and 3 but it also promotes creativity.

Zusammenfassung

Kultur ist ein wesentliches Element der menschlichen Evolution und ein einflussreicher Antrieb für die Entstehung höherer Intelligenz. Die soziale Kompetenz, notwendige Fähigkeiten von unserem sozio-kulturellen Umfeld zu lernen, ist eine fundamentale Komponente des menschlichen Charakters und ein Produkt der natürlichen Auslese. Dennoch ist Kultur kein Alleinstellungmerkmal des Menschen, wie die zunehmende Zahl von Nachweisen von Kultur bei anderen Tieren zeigt. Die entscheidende Frage ist, wie kulturelle Prozesse mit Kognition und der Evolution von Intelligenz verbunden sind, ob es also eine sogenannte kulturelle Intelligenz gibt. Das Prinzip hinter der *Kulturellen Intelligenzhypothese* ist, dass ein Individuum über umso bessere intellektuelle Fähigkeiten verfügt, je mehr Gelegenheit zu sozialem Lernen es im Laufe seiner Entwicklung erhält. Bei Arten, mit stark ausgeprägtem sozialen Lernen führt die natürliche Auslese der involvierten kognitiven Mechanismen im Laufe der Evolution zur Förderung der Intelligenz. Das primäre Ziel meiner Doktorarbeit ist es, die Kulturelle Intelligenzhypothese anhand eines unserer nächsten Verwandten, den Orang-Utans (*Pongo spp*), zu prüfen und die Rolle der kulturellen Prozesse in unserer gemeinsamen Evolutionsgeschichte zu untersuchen.

Genau wie beim Menschen besteht Kultur bei den Tieren aus verschiedenen Verhaltenstraditionen, die auf Innovationen aufgebaut sind. Um Kultur erklären zu können, müssen wir daher auch den Innovationsprozess verstehen. Es wird häufig behauptet, dass Innovationen als Reaktion auf Neues entstehen und dass dabei Arten, die innovativ sind, besonders neugierig (neophil) reagieren. Obwohl auch bei Orang-Utans die kulturelle Diversität aus verschiedenen Verhaltensinnovationen resultiert, ist noch wenig darüber bekannt, wie Orang-Utans sich gegenüber Neuem verhalten. Anhand empirischer Feldexperimente habe ich in meiner ersten Studie (*Kapitel 2*) untersucht, wie wilde Orang-Utans auf neue Objekte in ihrem Umfeld reagieren. Die Ergebnisse zeigen, dass wilde Orang-Utans eher konservativ sind und diese Objekte passiv meiden. Da Orang-Utans, wie die anderen Menschenaffen, zu den innovativsten nicht-menschlichen Arten gehören, sind diese Ergebnisse unerwartet. Anhand meiner Studie konnte ich zeigen, dass Orang-Utans es vermeiden unbekannte Objekte anzufassen (und daher nicht neophil sind), obwohl sie bereits bekannte Objekte in ihrem Lebensraum neugierig erforschen. Diese widersprüchlichen Ergebnisse lassen sich anhand des Konzeptes der Kulturellen Intelligenz erklären: ein Orang-Utan integriert Innovationen nicht in sein Verhaltensrepertoire indem er Neues erforscht, sondern durch soziales Lernen. Um zu ergründen, wie diese Umwelteinflüsse das Leben in Gefangenschaft beeinflussen, konfrontierte ich Zoo-Orang-Utans mit denselben neuen Objekten. In Gefangenschaft lebende Orang-Utans sind keinen natürlichen Gefahren ausgesetzt und haben beim Aufwachsen im Zoo durch die erhöhte Sozialität mit Artgenossenen und den Kontakt mit Tierpflegern, deutlich mehr Gelegenheit zu sozialem Lernen als in ihrem natürlichen Lebensraum. Im Gegensatz zu ihren wilden Artgenossenen zeigten die Zoo-

Individuen sofortiges Interesse an neuen Objekten. Dieser Unterschied in der Neophobie-Ausprägung wilder und gefangener Orang-Utans inspirierte mich dazu, eine umfangreiche Übersicht der bestehenden Literatur zu verfassen, in welcher ich die Variation in der Ausprägung von Neophobie bei weiteren Arten erkläre (*Kapitel 3*). In dieser Übersichtsstudie betone ich zuerst, dass jene Tiere, die wie die Menschenaffen einen langsamen Lebenslauf (Life-history) aufweisen, davon profitieren, sich in der freien Wildbahn konservativ zu verhalten. Dieses Verhalten begründet sich vermutlich darin, dass die Tiere viel stärker auf soziales Lernen als auf individuelle Exploration angewiesen sind. In Gefangenschaft hingegen, sind dieselben Arten neuen Objekten gegenüber eher aufgeschlossen (Neuophilie), da sie intensivere Sozialkontakte zu Artgenossen und eine vertrauten Umgang mit Menschen haben. Das Innovationsparadox kann folglich damit erklärt werden, wie sehr eine Art auf soziales Lernen angewiesen ist und spricht somit für die Kulturelle Intelligenzhypothese.

In meinem vierten Kapitel untersuche ich die Bedeutung einer starken Anpassung an soziales Lernen und teste die Kulturelle Intelligenzhypothese empirisch. Da kulturelle Arten ihre Fähigkeiten durch soziales Lernen entwickeln, ist anzunehmen, dass eine starke natürliche Auslese in Bezug auf Lernmechanismen stattgefunden hat. Bei Arten, deren soziale Umwelt systematisch vielfältige Lernmöglichkeiten anbietet, sollte sich folglich im Laufe der Evolutionsgeschichte höhere Intelligenz entwickelt haben, die sich auch in einer Zunahme der Gehirngrösse widerspiegelt. Die Überprüfung dieser evolutionären Perspektive der Kulturellen Intelligenzhypothese war mein Hauptziel in Kapitel 4. Die beiden Orang-Utan Arten, der Sumatra- (*Pongo abelii*) und der Borneo-Orang-Utan (*Pongo pygmaeus*), haben im Laufe der Evolution verschiedene soziale und ökologische Umweltbedingungen erfahren, was dazu geführt hat, dass der Sumatra-Orang-Utan über eine höhere soziale Toleranz mit häufigeren Gelegenheiten für soziales Lernen verfügt. Dadurch wurde wiederum die Kumulierung neuer Fähigkeiten in der Population ermöglicht. Um den Einfluss von Unterschieden hinsichtlich sozialer und ökologischen Faktoren des natürlichen Lebensraums kontrollieren zu können, habe ich meine Studie über Unterschiede der kognitiven Fähigkeiten der beiden *Pongo* Arten in mehreren Zoos durchgeführt. Die homogenen Umweltverhältnisse der Zoos ermöglichten es mir, intrinsische Unterschiede zwischen den beiden Arten zu aufzudecken. Meine Ergebnisse illustrieren das ultimative Produkt kultureller Intelligenz und zeigen klare Unterschiede im Bereich der intrinsischen Lernkapazität der beiden Arten. Der Sumatra-Orang-Utan besitzt dabei die besseren Fähigkeiten, Probleme zu lösen als der Borneo-Orang-Utan. Diesen Artunterschied konnte ich nicht nur hinsichtlich der kognitiven Leistungen, sondern auch des Explorationsstils und der inhibitorischen Kontrolle zur Unterdrückung bestehender Verhaltenstendenzen zeigen. Ich schliesse daraus, dass der Sumatra-Orang-Utan im Vergleich zum Borneo-Orang-Utan vermutlich eine stärkere natürliche Auslese hinsichtlich jener Mechanismen erfahren hat, die dem Lernen zugrunde liegen.

Mein fünftes und letztes Kapitel setzt sich ebenfalls mit der Frage auseinander, wie ein Leben in Gefangenschaft kognitive Fähigkeiten beeinflusst und wie individuelle Unterschiede der

Problemlösefähigkeiten zustande kommen. In Zusammenarbeit mit meiner Arbeitskollegin Laura Damerius, habe ich die Reaktionen auf Neues, das Explorationsverhalten und die kognitiven Fähigkeiten von Orang-Utans mittels einer großen Stichprobe aus mehreren Zoos und Auffangstationen gemessen. Unsere Stichprobe bestand aus Individuen, die unterschiedliche Aufzuchtbedingungen erfahren und unterschiedlich viel Zeit mit Menschen verbracht hatten - Faktoren von denen angenommen wird, dass sie kognitive Fähigkeiten beeinflussen. Zusätzlich haben wir ein Instrument entwickelt, welches die Reaktionen eines Einzelindividuums auf den Menschen misst. Es handelt sich dabei um den sogenannten *Human Orientation Index* (HOI). Dieser Methode erlaubten uns mit einem einfachen Test zu untersuchen wie fest jedes Individuum auf Menschen fokussiert ist und weder sie auf Menschen mit positiven oder negativen verhalten reagieren. Wir konnten zeigen, dass unterschiedliche Aufzucht- und Haltungsbedingungen keinen Einfluss auf die kognitive Leistungsfähigkeit der Orang-Utans hatten, wohingegen unterschiedliche Reaktionen auf den Menschen kognitive Leistungsunterschiede am besten voraussagten. Im Einklang mit der Kulturellen Intelligenzhypothese zeigten Individuen mit einem höherem HOI-index ein besseres Aufmerksamkeitsvermögen und bessere Problemlösefähigkeiten. In Gefangenschaft aufwachsende Affen nutzen also nicht nur den Menschen als soziales Vorbild, was zu verminderter Neophobie führt (*Kapitel 1 und 2*), sondern der Kontakt mit Menschen trägt darüber hinaus auch zu kreativerem Verhalten bei.

Acknowledgements

I owe my thanks to each and every person who has been part of my life during my graduate years. In one way or another all of you have inspired me, supported me and encouraged me through any ups and downs on the road.

I would like to express my greatest thanks to my advisor *Carel van Schaik*. Throughout both difficult and successful moments I always felt not only completely supported but also inspired by his enthusiasm for the project. I consider myself lucky to have shared many working years with Carel and he surely has raised a scientific passion in me that I will carry with me for life. I would also like to especially thank *Maria van Noordwijk* for always engaging in the project providing feedback and help, but mostly for being the "office Mum" who always took her time to listen when one is in need. I have many reasons to thank *Erik Willems*. To start with the formal ones, he has contributed with great statistical help for the majority of my work but beyond that he has been my roommate, my shoulder to cry on, my friend to enjoy life outside the office with or maybe best described as something like a brother to me. There are equally many reasons for me to thank *Laura Damerius*. Our projects have been going scientifically hand in hand and she has been a loyal, reliable and committed collaborator. Not only do I thank Laura for our shared achievements but in fact she deserves an award for withstanding my ups and downs and emotional eruptions in our office, which tended to accumulate toward the end of the PhD.

I would like to thank my committee members *Judith Burkart* and *Josep Call*. Judith has provided great support and valuable ideas throughout the experimental work with the orangutans and Josep especially for his hospitality and involvement as I was allowed to conduct data at the Wolfgang Köhler primate center in Leipzig. I am also very grateful to *Sonja Koski* for her valuable contributions as a co-author on my second paper and of course her Finnish "sisu" that always inspired me. *Claudia Zebib-Brunner* deserves an especially big thank you for endless helpfulness with all bureaucratic and financial matters. I also thank *Marcus Gisi* for his help to solve any technical issues and *Tony Weingrill* and the graduate campus for the organization of the Life science PhD program, especially for the joyful times at the PhD retreats.

As the first year of my PhD was spent in Indonesia at the research sites of Tuanan and Suaq Balimbing, I would like to heart fully thank all the people involved in keeping the sites running and everyone working hard in the forests, particularly all the field assistants; *Fikar, Izumi, Dimas, Sahrol, Abuk* and *Rahmad* who climbed all those high trees to manage my camera traps. *Nicole Zweifel* for sharing some memorable moments in Tuanan with me from jungle-fondue to discovering of the weirdest insects we could find in the forest. Many thanks to *Caroline Schuppli* and *Brigitte Spillmann* for the amazing times

at Suaq Balimbing. Caroline was a great field companion and I also owe my thanks for her contribution to my first paper. Brigitte has during all these years been a great support and a great friend in many ways, endless discussions until the early morning hours, shared sleepless nights during conferences and everyday mini-breaks that have helped me stay on track many times. But beyond that I owe my sincere thanks to Brigitte for literally saving my life by escorting me to the hospital as I fell ill with malaria and dengue fever. Also a heartfelt thank you to both Brigitte and *Serge Wich* for caring for me during my weeks in the hospital, supplying me with food that I could bring myself to eat as my appetite and body strength had vanished. During that most challenging time I have ever experienced I would also like to acknowledge my dear friend *Anto*, who regularly visited and pampered me when I was at the bottom as well as my own mother who just like a miracle appeared next to my hospital bed all the way from Finland to Indonesia.

As my project took a radical but very insightful turn I would like to thank all the zoos that welcomed me to perform my cognitive tests with their orangutans; *Zoo Zürich, Zoo Dortmund, Twycross Zoo, Durrell Wildlife Trust, Allwetterzoo Münster, Zoo Basel, Apenheul Primate Park, Wolfgang Köhler Primate Center at Leipzig Zoo, Blackpool Zoo* and *Paignton Zoo*. Foremost I thank all the orangutan caretakers who let me into their daily routines, helped me out with carrying out my experiments and provided me with a friendly and enriched working experience in the zoos. This project would not have been possible without their help. In particular I thank *Ilona Schappert, Charlotte McDonald, Gordon Hunt, Simone Schehka, Adrian Baumeyer, Thomas Bionda, Laura Salanki, Matthew Webb, Johannes Grossmann* and *Hanna Petschauer* for their collaboration throughout my time collecting data across such a wide range of zoos.

My sincerest thanks are for all the foundations that have funded my research: *A. H. Schultz Foundation, Paul Schiller Foundation* and *the Claraz Donation* in Switzerland and from my homeland Finland: *Waldemar von Frenckells Foundation, Ella and Georgh Ehrnrooths Foundation, Otto A. Malms Donationsfond, Nordenskiöld Samfundet, Oskar Öflunds Foundation* and *Svensk Österbottniska Samfundet* as well as two international contributions from *the International Primatological Society* and *the Orangutan Foundation* in the United Kingdom. Financial support from all these foundations has been crucial for me and without the generous help from any of them I would have never been able to practice such a large-scale data collection and finish my PhD, so once again my sincerest gratefulness to all my funding parties.

Because my project required me to be constantly on the move between zoos the anthropological institute has felt like a stable home base for me and it has provided a professional but family-like work atmosphere. My warmest thanks go to all of the people at the AIM who I have been pleased to have as my colleagues throughout all these years.

Finally, with all my love I would like to thank my family: *Fredrik, Karin, Björn* and *Erik Forss*. Not only have they supported me from the start to the end but also enthusiastically listened to all my orangutan stories and helped me to feel proud of my accomplishments. I am thankful that they had the opportunity to visit me both out in the rainforest as well as in the zoos, to gain an understanding of why I love what I do. Moreover, I thank my father for all his practical help with building the test apparatuses and converting video clips and my mother for her interest in orangutans and their conservation issues.

To end, I will also dedicate a thought to all the individual orangutans I was fortunate to work with. From the wild to all the zoos there were over one hundred, and I remember all their names and individualities. For me as a researcher - interested in understanding their minds - I am very thankful for the two perspectives I gained: observe them in their natural habitat and actually engage and work together with them in the zoos.

Table of Contents

CHAPTER 3: THE PARADOX OF NEOPHOBIC EXPLORERS: THE SOCIAL INFORMATION HYPOTHESIS

CHAPTER 4: COGNITIVE DIFFERENCES BETWEEN ORANGUTAN SPECIES: A TEST OF THE CULTURAL INTELLIGENCE HYPOTHESIS

CHAPTER 5: HUMAN INDUCED CURIOSITY PREDICTS COGNITIVE PERFORMANCE IN ORANGUTANS

Chapter 1

General Introduction

1.1 The evolution of intelligence

Without a doubt humans stand out among animals with regards to our advanced cognitive capacities, innovativeness and flexibility, in other words those abilities we like to call intelligence. While humans are exceptional in the extent to which we possess such higher cognitive capacities, we are far from unique in being an intelligent species. To understand what the concept of intelligence means and why it became so extremely prominent in our own linage is one of the most intriguing but challenging topics in evolutionary research. Throughout this dissertation I will refer to intelligence as defined by Rumbaugh and Washburn (2003): "*the ability of using acquired skills and knowledge innovatively, to unique advantages in solving novel problems*".

While intelligence has been shown to partly consist of a heritable, genetically determined component in humans (Bates *et al*., 2013; Bouchard 2004; Deary *et al*., 2009; Davies *et al*., 2011; Nisbett *et al*., 2012; Turkheimer *et al*., 2013; Joshi *et al*., 2015) but also in other animals (Galsworthy *et al*., 2005; Hopkins *et al*., 2014), it most certainly also represents effects of experiences acquired through learning processes (Wilson, 1991; Reader & Laland, 2002; Whiten & van Schaik, 2007; van Schaik & Burkart, 2011; Galef, 2015). Consequently, in order to understand evolution of intelligence we need to improve our insight into the - *what* and *how* - underlying mechanisms promote learning and information processing in animals.

Evolutionary histories, characterized by distinctive selective pressures, have produced species differences in brain size and cognitive plasticity. In species exhibiting high plasticity, environmental factors generate broad intraspecific variation in cognitive abilities. Accordingly, *species* differ in cognitive flexibility and further *individuals* within species differ depending on past experiences. Although constructed somewhat differently across animal taxa, the brain is responsible for information processing and cognitive functions. Since enlarged brains are connected with both increased cognitive capacities and flexibility (Byrne & Whiten, 1988; Harvey, 1990; Dunbar, 1995; Byrne, 1997; Reader & Laland, 2002; Johnson *et al*., 2002; Lefebvre *et al*., 2004; Deaner *et al*., 2007), correspondingly, entangled with the evolution of intelligence is of course an interest in the evolution of larger brains (Isler & van Schaik, 2009; Navarette *et al*., 2011; van Schaik *et al*., 2012). Because brain expansion plays such a central role in human evolution, factors promoting intelligence have received intense interest, which has resulted in multiple hypotheses, all of which aim to explain the selection pressures responsible for the evolution of intelligence, as well as its convergent presence in animal taxa.

Among these ideas, two have become most prominent. First, Richard Byrne put forward intelligence as a response to ecological challenges, evolved to succeed in extractive foraging - an idea referred to as *the Technical- or Ecological Intelligence Hypothesis*. The hypothesis assumes that animals confronted

with a challenging foraging niche, such as food items that are hidden and require pre-processing (e.g. extractive foraging), experience selection for higher-level cognition (Byrne, 1997). Second, based upon work suggesting that the cognitively most demanding aspects of primate life is their living in complex social groups (Humphrey, 1976), *the Machiavellian Intelligence Hypothesis* covers the connection between intelligence and the complexity of an animal's social environment, and thus argues intelligence evolved from the need to manage successfully in an ever-changing, and complicated social environment (Whiten & Byrne, 1988). In support of Machiavellian intelligence, correlated evolution between group size and the relative size of the neocortex ratio has been established among primates (Aiello & Dunbar, 1993). However, because many non-primate species also live in equally complex social groups, but are small-brained (Holekamp, 2007), an updated version of this idea states that the demands of maintaining pair bonds and social coordination have selected for larger brain size (Dunbar & Shultz, 2007).

While both ecological and social challenges surely create selective pressures shaping the evolution of intelligence, it is highly debated to what extent cognitive abilities among non-human animals are domain-specific responses to particular ecological or social challenges rather than an expression of more human-like, general and flexible capacity to learn, commonly referred to as 'g' (Carroll, 1993; Reader & Laland, 2002; Deary *et al*., 2010; van Schaik & Burkart, 2011; Major *et al*., 2012; Burkart *et al*., in review). Reader and Laland (2002) argued that selection on a general ability to learn is more efficient as an adaptive advantage in itself, rather than as a consequence of selection on separate domains. A focus on selection pressure targeting learning ability per se, combined with the breakthrough of extensive research on animal cultures, shifted the attention toward how underlying cultural processes link to cognition and the evolution of intelligence: i.e. *cultural intelligence* (Tomasello *et al*., 1993; Tomasello, 2000; Whiten, 2000; Herrmann *et al*., 2007; Whiten & van Schaik, 2007; Reader *et al*., 2011; van Schaik & Burkart, 2011).

At first, *the Cultural Intelligence Hypothesis* was presented as a concept describing specialized socio-cognitive skills unique to humans, in order to cope with our enriched cultural niche (Tomasello, 1999); or as Alice Roberts quipped: "*fish are born expecting water, and humans are born expecting culture*". The quote symbolizes the nature of cultural complexity in humans, founded strongly upon specialized socio-cognitive abilities enabling exchange of knowledge across our cooperative and social lifestyle (Vygotsky, 1978; Tomasello *et al*., 1993; Tomasello, 2000; Herrmann *et al*., 2007). Although this hypothesis was initially thought to apply to humans only, the context of cultural intelligence has since been expanded to all non-human animals adapted to rely on social learning (Whiten & van Schaik, 2007; van Schaik & Burkart, 2011). *The Cultural Intelligence Hypothesis*, as argued by van Schaik and Burkart (2011), expects intelligence to be affected by culture and underlying learning mechanisms on two different time scales. Over evolutionary time, *the Cultural Intelligence Hypothesis* assumes that opportunities for social learning influence selection on the underlying learning processes. Because

selection on the effectiveness of social learning is largely selection on asocial learning abilities, species with systematically richer social environment may over time evolve to become more intelligent, reflected by larger brain size (van Schaik & Burkhart, 2011). Secondly, *the Cultural Intelligence Hypothesis* also predicts an influence on intelligence during the lifetime of an individual, by stating that individuals within a species (with very similar brain size and behavioral predispositions) show variation in cognitive performance and learning ability (intelligence) depending on the opportunities for social learning experienced during ontogeny. Thus, individuals growing up in a stimulus-rich environment can reach a higher degree of intelligence than an individual of the same species exposed to poor social conditions during the developmental phase.

1.2 Orangutans as a model taxon

The purpose of my dissertation was to test the *Cultural Intelligence Hypothesis* as well as the related sub-hypothesis of the captivity effect (see below) by using orangutans as a model taxon. Orangutans are ideal for this objective. The genus *Pongo* contains some of our closest living relatives, representing two separate species where social learning plays an evident role in how they acquire their adult competence and culture-specific foraging niche, portrayed by broad diets and complex food processing techniques (van Schaik *et al*., 1996; van Schaik *et al*., 2003; Jaeggi *et al*., 2010; Schuppli *et al*., 2012; Schuppli *et al*., in prep.). Thus there are evident reasons to why orangutans need to develop intelligence. Orangutans live long lives characterized by a very slow life history, reaching adult skill competence only around the age of 12 (Schuppli *et al*., in prep.) and first reproduction around the age of 15 (Knott *et al*., 2009), which means they are the slowest-lived among non-human primates. Orangutans' extended developmental phase is described by a long lasting tolerant mother-infant connection, which provides the infant with plenty of opportunities to learn the specific foraging complexity.

Moreover, orangutan sociality varies among habitats and also species. The often volcanic and generally more fertile soils of Sumatra generate higher plant productivity and fruit availability than on Borneo (Marshall *et al*., 2009). This higher habitat productivity is the foundation for fundamental differences in socio-ecology between *Pongo abelii* and the *Pongo pygmaeus* species, allowing for higher densities within the populations of orangutans in Sumatra than Borneo. Consequently, the Sumatran orangutans show higher degrees of sociality and gregariousness, which also allows for intensified social transmission of skills and opportunities for social learning (van Schaik, 1999; Wich *et al*., 2006). As a result the cultural repertoires of the different orangutan species studied to date contain a broader dietary range and more complex feeding techniques amongst the Sumatran populations (van Schaik *et al*., 2003; Schuppli *et al*., in prep.). A further consequence of habitat productivity and feeding ecology is an increase in cranial capacity, and relative brain size from east to west across the range of orangutan habitats. Thus, the largest cranial capacity is documented from *Pongo abelii*, whereas *Pongo pygmaeus*

morio have significantly smaller brain sizes (Taylor & van Schaik, 2007). The significant differences in socio-ecological conditions gives us an excellent foundation for testing the evolutionary prediction of the *Cultural Intelligence Hypothesis*. However, because of the diverse biogeography any intrinsic difference between the two *Pongo* species is impossible to assess in their natural habitats, which is why a large part of my dissertation work was carried out under zoo conditions.

The data collection on wild orangutans was conducted between July 2010 and April 2011 at two different study sites run by the Anthropological Institute and Museum of Zurich University: Suaq Balimbing, Sumatra and Tuanan, Borneo. Suaq Balimbing constitutes of a research area of 640 hectares located in the Gunung Leuser ecosystem in the province of Aceh in north Sumatra (3°42'N, 97°26'E) with an orangutan density of estimated 7 individuals per km^2. The Tuanan research areal is situated in the Mawas reserve of central Kalimantan (2°09'S, 114°26'E) and reach over 1000 hectares with a density of 4 orangutans per km^2.

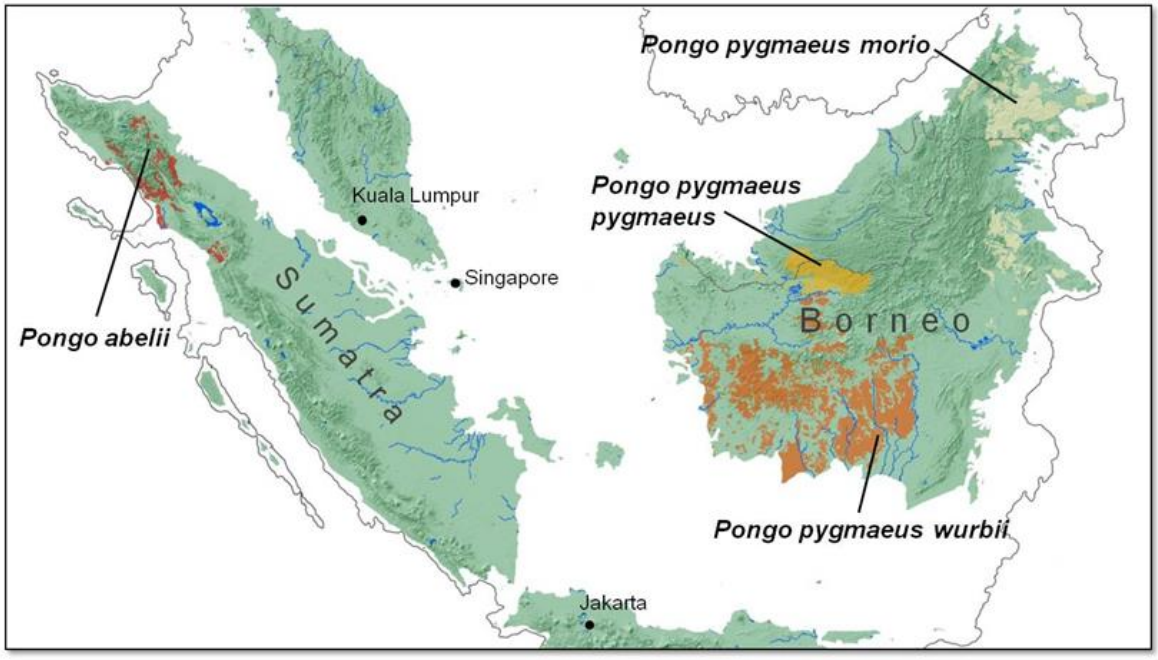

Figure 2: Orangutan distribution and species division in their natural habitat (*map: E. Willems*).

While the data conducted with field experiments in the natural habitat allowed me to investigate the ecological relevance of novelty response in orangutans, the data collection on zoo housed individuals allowed me to examine exploration and problem-solving abilities in greater detail and the underlying cognitive mechanisms. Therefore, the second data set upon which my thesis is constructed was conducted at the following European zoological gardens housing orangutans from both species of *Pongo abelii* and *Pongo pygmaeus*: Zürich Zoo, Zoo Dortmund, Durrell Wildlife Trust, Twyycross Zoo, Allwetter Zoo Münster, Zoo Basel, Apenheul Primate Park, Paignton Zoo, Blackpool Zoo and Wolfgang Köhler Primate Center at Leipzig Zoo (Table 1).

Because the division of the Bornean *Pongo* taxa into three subspecies, *Pongo pygmaeus pygmaeus*, *Pongo pygmaeus wurmbii* and *Pongo pygmaeus morio*, was recently established (Zhi *et al*., 1996; Warren *et al*., 2001; Steiper, 2006), these subspecies of Bornean orangutans have not been managed separately in zoos and thus represent a general *Pongo pygmaeus spp*. Therefore zoo orangutans from Borneo are not monophyletic and probably carries genes from all three subspecies, which future genomic work will be able to revise (Greminger, 2015). The experimental study was supported by the British and Irish association for zoos and aquariums, BIAZA, and fully comply with the ethical guidelines for zoo housed non-human primates of each study facility, the European Directive 2010/63/EU and are approved by the ethics committee of the University of Zurich in Switzerland.

Table 1: Zoological gardens where data collection took place.

Zoo	Species	Time of study	Research purpose
Zürich zoo	*Pongo abelii*	December 2011	Novelty response
Twycross zoo	*Pongo pygmaeus*	January- February 2013	Physical cognition
Allwetter zoo münster	*Pongo pygmaeus*	April- May 2013	Physical cognition
Apenheul Primate Park	*Pongo pygmaeus*	January- February 2014	Physical cognition
Blackpool zoo	*Pongo pygmaeus*	January 2015	Physical cognition
Paignton zoo	*Pongo pygmaeus*	February 2015	Physical cognition
Dortmund zoo	*Pongo abelii*	November- December 2012	Physical cognition
Durrell Wildlife Trust	*Pongo abelii*	March 2013	Physical cognition
Basel zoo	*Pongo abelii*	November 2013	Physical cognition
Leipzig zoo	*Pongo abelii*	March 2014	Physical cognition

1.3 What is animal intelligence and how can we measure it?

Human intelligence is typically measured with multiple tests assaying an array of cognitive abilities such as memory span, processing speed, visualization ability, mathematical achievement, verbal comprehension, spatial orientation etc., commonly classified together as a general intelligence factor 'g' (Plomin, 2001; Colom *et al*., 2006; Gläscher *et al*., 2010; Burgess *et al*., 2011). Thus as we are interested in the evolutionary history of this ability, we need to measure comparable traits in non-human animals. Since animals cannot partake in intelligence tests requiring language or advanced mathematical skills, the focus lies on detecting and measuring behaviors that require cognitive capacities. In nature animals use their cognitive abilities in various ways to overcome both ecological challenges, related to foraging and spatial orientation, as well as managing and maintaining social interactions.

One proxy for animal intelligence, which has been studied both in the wild and in the lab, is the concept of innovation. An influential and widely adopted definition of innovation was given by Kummer and Goodall (1985): "*a solution to a novel problem or a novel solution to an old problem*". More recently van Schaik *et al* (2016) refer to innovativeness as "*novel behaviors brought into a population through an individual invention*" and link innovation capability to problem-solving skills and behavioral flexibility. In nature innovations remain rare and their emergence is critically influenced by ecological factors (van Schaik *et al*., 2016). Furthermore, a positive relationship between innovativeness and brain size has been established across species in birds (Lefebvre *et al*., 1997; Timmermans *et al*., 2000; Sol *et al*., 2005; Overington *et al*., 2009) and primates (Reader & Laland, 2002), supporting its validation as a measurement for animal intelligence (Reader & Laland, 2002; Lefebvre *et al*., 2004; Reader *et al*., 2011).

Innovativeness and underlying mechanisms have been extensively studied in captive settings where animals are presented with novel problems. This approach is increasingly also applied to wild populations (Webster & Lefebvre, 2001; Bouchard *et al*., 2007; Laidre, 2007; Liker & Bókony, 2009; Morand-Ferron *et al*., 2011; Overington *et al*., 2011; Benson-Amram & Holekamp, 2012; Thornton & Samson, 2012). However, problem-solving tasks, which are introduced only once for each animal, have been criticized for not capturing true individual cognitive variation and the lack ecological relevance (Rowe & Healy, 2014; Thornton *et al*., 2014). In nature it is hard to control for ecological influences and different experiences any individuals carry with them. In order to detect true differences in innovative problem solving, a task ideally represent a novel problem, which would not be encountered in the natural habitat, and be performed under identical conditions for all participants. Thus, in order to understand the process of innovativeness, natural observations provide insight in under what ecological conditions innovations occur and further experimental settings in captivity can expose animals with truly novel challenges, which are of great importance to complete the picture of what underlies an individual's capacity to invent.

1.4 How can intelligence evolve?

The main adaptive value of intelligence is phenotypic plasticity, allowing for inter- and intraspecific variation under variable external conditions. Thus, because the end product of intelligence is acquired through learning, any species expressing higher levels of intelligence has to have undergone selection on learning mechanisms. Rumbaugh and Washburn (2003) described learning as "*the foundation of intelligence*". Moreover, the *learning to learn* effect (Heinrich, 2016) illustrates the ability to modify and adjust behavior according to sensory information and inputs from one's environment.

When individuals live in social groups they can not only adjust their behavior and learn from environmental inputs but also from other individuals or the products of their actions, in other words

through socially meditated learning. First, socially facilitated learning allows for a naïve individual to use information in order to attend to relevant stimuli. Second, through social learning fitness-enhancing skills can be acquired in both a faster and safer way than through asocial learning, which can be both time and energy consuming but also involves potential risks during independent exploration. Third, social learning enables individuals to directly construct their knowledge around an innovation originated by another, and thus social learning promotes conditions resulting in accumulation of skills and modification of previous innovations. As a result, social learning should favor the evolution of intelligence because skills necessary for fitness are acquired more efficiently and over time improve the learning-to-learn ability, especially because social learning ability improves asocial learning proficiency as well, as a result of many overlapping psychological mechanisms of information processing (Heyes, 2011; van Schaik & Burkart, 2011).

The Cultural Intelligence Hypothesis predicts that social learning is essential to the evolution of intelligence. Consequently, individuals that experience a high frequency of opportunities for social learning during development, should not only acquire more skills, but also become more intelligent. Thereby, asocial learning ability may well initially not have been directly selected for, although its function as a byproduct is of adaptive value, as it generates a higher innovative ability. This in turn can eventually lead to new innovations, which boost the cultural repertoire through an increase in the skill pool, which also in turn generates more opportunities for social learning and promotes selection for it. This loop of responses, all involving learning mechanisms, is what constitutes the evolutionary prediction of *the Cultural Intelligence Hypothesis*. The evolutionary perspective argues that species with a long history of enriched opportunities for social learning may over time improve both social and asocial learning abilities and therefore intelligence should be higher where opportunities for social learning have persistently been more frequent.

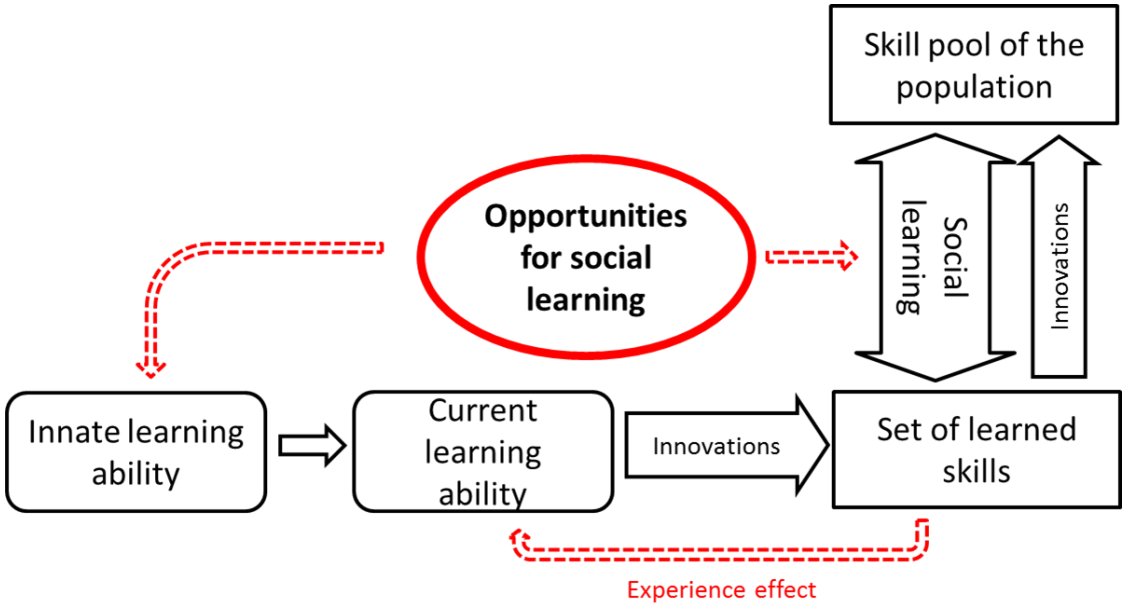

Figure 1: The model of learning processes involved in cultural intelligence (*Adapted from van Schaik and Burkart, 2011*).

1.5 The effects of captivity – what can we learn?

Animals housed in human structured environments differ a great deal from their wild conspecifics. Physiological differences caused by improved nutrition affect body condition and the rate of development (Hediger, 2013). Wild and captive individuals may also differ in endocrine profiles: in some species, captive individuals show higher cortisol levels compared to free living conspecifics (Rangel-Negrín *et al*., 2009; Weingrill *et al*., 2011). These differences may reflect the fact that the social conditions in captivity do not reflect their natural social structure in the wild (Weingrill *et al*., 2011). In this dissertation, however, I will ignore such physiological differences and focus on behavioral ones. Thus *the captivity effect* I will refer to throughout my thesis describes cognitive variation within species as a consequence of factors related to living in a captive habitat. Captive individuals differ in their cognitive skills and may even develop a different mindset than they would in their natural habitat (Call & Tomasello, 1996; Savage-Rumbaugh *et al*., 2007). Although we must always study animal behavior in the natural world to understand its functional or adaptive aspects, the differences between wild and captive can contribute significantly to our understanding of phenotypic plasticity or the width of reaction norms. In particular, contrasts in cognition provide us with insights into how underlying psychological mechanisms develop depending on both physical and social environmental inputs.

Among extractive foragers tool use is one cognitively regulated behavior boosted in captive conditions. Some species that do not generally use tools in their natural habitat do so in captivity (Bentley-Condit & Smith, 2010)—a phenomenon especially pronounced in both primates (Beck, 1972; Beck, 1976; Jordan, 1982; Boysen *et al*., 1999; Hihara *et al*., 2003; Santos *et al*., 2006; Gruber *et al*., 2010) and birds (Borsari & Ottoni, 2005; Bird & Emery, 2009; Seed *et al*., 2006; Auersperg *et al*., 2011; Gajdon *et al*., 2011). Second, tool use tends to become more complex and diverse in captivity, a fact also found to be true for both primates (Haslam, 2013) and birds (Auersperg *et al*., 2011; Wimpenny *et al*., 2011). Some species that use simpler tools in the wild, modify and even manufacture tools in under captive settings (Hunt, 1996; Lehner *et al*., 2011; Shumaker *et al*., 2011).

Many factors combined are believed to contribute to such an intensification of tool use in captivity. First, the absence of predators and a general risk free habitat increase free time and provide a reduction in cognitive load, which in turn promote explorative behaviors (Kummer & Goodall, 1985; Haslam, 2013; van Schaik *et al.*, 2016). Second, arboreal species found in captivity increase their terrestriality, which is also argued to promote tool use (Meulman *et al*., 2012). As a third factor intensified social conditions, as often found in captivity, stimulate social transmission processes once a behavior has been invented (Haslam, 2013).

The same factors influencing tool use can also cause increased exploration tendency and innovativeness in captive versus wild individuals, as reported in primates (Laidre, 2007; Russon *et al*.,

2009; Lehner *et al*., 2010; Russon *et al*., 2010). When studied, other animals also show the same pattern: captive hyenas were more habituated towards man-made objects, and consequently showed lowered neophobia toward the test apparatus, which resulted in higher success in problem-solving compared to wild conspecifics (Benson-Amram *et al*., 2013). The same pattern was expressed in orangutans, when wild and captive individuals were compared (Forss *et al*., 2015). As a matter of fact, a lot of the cognitive differences between wild and captive individuals may be a direct or indirect consequence of the reduced neophobia observed in captivity.

Thus in sum, cognitive differences between wild and captive primates have so far been attributed to reduced ecological costs, whereas social and developmental influences have - up to now – been understudied. Because primates have evolved to pay attention to others' actions, captivity offers increased learning opportunities, which also extends beyond conspecifics to humans. The question remains whether this close contact with humans reflects a fundamental change in cognition. However, if it does we can use it as a tool to improve our knowledge of the plasticity of experience-based cognition in non-human species. Consequently, the *Cultural Intelligence Hypothesis* is also testable using the captivity effect. A captive environment in general consist of intense social contacts, including more nearby conspecifics than in the wild and animal keepers that act as additional role models. Because different captive conditions, such as variable housing and rearing histories, generate variation in the amount of social- and skill learning inputs, variation in intelligence across captive housed individuals may vary. This diversity provides us with excellent conditions for testing the hypothesis and the impact of learning opportunities during an individual's lifetime.

1.6 Aims and content of the thesis

This dissertation is based upon four main chapters representing original research. Each chapter has been written to stand independently and either has been or will be published in scientific journals. Three chapters are founded on empirical work performed with both wild and captive orangutans and one chapter consist of an extensive review of the current literature.

This dissertation is divided into two major parts. In the first part I examine response to novelty and its link to innovation and social learning. In the second part I specifically test *the Cultural Intelligence Hypothesis* from two distinct perspectives: an evolutionary one (*chapter 3*) and a developmental one (*chapter 4*). In addition, throughout my dissertation the captivity effect plays an important role. I am specifically assessing the influence of a captive lifestyle on psychological mechanisms underlying novelty response and cognitive performance (*chapter 1 & 4*), whilst in chapter 3 captive conditions are used to control for biographic diversity and makes it possible to conduct an otherwise impossible honest comparative study of the cognition of the two *Pongo* species.

1.6.1 Novelty response

How animals respond to novelty is highly interesting because it presents animals with new potential benefits in terms of niche expansion and resource use. However, responding to something novel also carries great risks and thus animals may differ in willingness to face such situations. Because neophilia has been reported to correlate with innovativeness (Seferta *et al*., 2001; Webster & Lefebvre, 2001; Bouchard, 2002; Reader, 2003), a positive novelty response has widely been assumed an important step toward innovation, and because large-brained species are highly innovative it is often believed they exhibit a drive to explore novelty (Sol *et al*., 2005; Overington et al. 2009). This assumption implies that innovations arise through an adaptive pathway on the individual level involving curiosity and novelty attraction. In most natural habitats attraction toward novelty is risky, and thus can only evolve where risk levels are reduced and investment in individual exploration is rewarding. Alternatively, innovations result from a social pathway, where individuals incorporate and modify novel behaviors under influence of social cues.

In my first chapter I examined response to novelty in an innovative species, the orangutan. Systematic comparisons between wild and captive individuals of the same species is to date still very rare, although they are of great importance in our understanding of animal cognition. Furthermore, novelty response has never before been methodically assessed in a great ape species, especially not in their natural habitat. I started off by performing field experiments with wild orangutans on both the islands of Sumatra and Borneo. Since wild but habituated great apes can attend to humans one has to be cautious not to contaminate their natural behavior whilst introducing field experiments. Consequently field experiments introducing novelty to great apes are rare, and very little is known on how exactly they respond to new things, especially without any humans present. I was able to investigate the topic by using motion-triggered video camera traps, monitoring multiple locations in the forest canopy, complemented by focal follows of individuals. Because wild orangutans are known to produce innovations, and among the Sumatran species even more so than the Bornean (van Schaik *et al*., 1996; van Schaik & Knott, 2001; van Schaik, 2004; van Schaik *et al*., 2006), one would initially expect them to respond more positively towards novelty than their Bornean conspecifics. Remarkably the results reported orangutans of both species to be extremely conservative and indifferent towards novelty, be it potential food or objects. In contrast, a systematic control study on captive housed orangutans that relied on the same novel items revealed loss of neophobia. Zoo-housed orangutans reacted with a direct interest in novel items presented to them. These results document the paradox of an innovative species showing very low novelty response in the wild, but a contrasting novelty interest in captivity (*chapter 2*).

My findings from the empirical study served as inspiration for the third chapter, an extensive literature review examining novelty response across taxa, with special focus of the paradoxical combination of

high exploration tendency and high neophobia, which seems to best describe species such as the great apes. In the review I argue that species with slow life history and relying on social learning can in fact afford to be rather neophobic in their natural habitat, which is crucial for our understanding of the significance and the behavioral outcomes of social learning (*chapter 3*). If innovative species, such as the great apes are not naturally particularly novelty-seeking, the pathway to innovation through novelty response is prevented in this lineage. Thus, such species are more likely to acquire their innovations in other ways, and presumably often through socially mediated learning, which also makes sense in the context of cultural intelligence.

1.6.2 Testing the Cultural Intelligence Hypothesis

The second part of my dissertation concerns the consequences of strong reliance on social learning. When social learning is adaptive, the selection pressure on improving it must have been high. Accordingly the *Cultural Intelligence Hypothesis* predicts that species systematically experiencing a higher number of social learning opportunities will end up evolving higher cognitive capacity. First, I aimed to test the evolutionary prediction of the *Cultural Intelligence Hypothesis* by comparing cognitive abilities between two closely related species (*Pongo abelii* and *Pongo pygmaeus*) that have over an evolutionary time scale experienced variation in both niche complexity, sociality and thus underlying occasions for learning opportunities (*chapter 4*). In order to identify intrinsic differences between the two species, I carried out the comparison under constant zoo conditions. This allowed me to control for ecological and social variation, which inevitably generates species differences in multiple behavioral domains in the wild and thus confounds any comparisons of intrinsic differences.

The zoo environment in which I performed my experimental study on cognition, also allowed me to examine the captivity effect in greater detail. Some species and definitely great apes, are able to attend to humans as a source of social information and thus social inputs are extended beyond conspecifics alone (Russon *et al*., 1998; Russon, 2003; Forss *et al*., 2015) and may serve as guidance for acquiring certain cognitively constructed skills. This may be especially pronounced in enculturated great apes, who also develop an enhanced ability in understanding human communicative actions (Call & Tomasello, 1996; Tomasello & Call, 2004).

The second level at which I tested the *Cultural Intelligence Hypothesis* was to test the prediction that captive orangutans should vary in intelligence (problem-solving and learning abilities) depending on their social experiences during ontogeny. This fifth chapter of my dissertation is the outcome of a close collaboration with my colleague Laura Damerius. By combining our separate data sets collected with identical methods, we could study within-taxon variation in intelligence across different captive conditions, with individual backgrounds ranging from recent arrivals from the wild to those that had spent their entire life in captivity, in rehabilitation centers on Sumatra and Borneo and throughout

European zoos. Our large sample included over 100 individuals, which therefore provided us with excellent conditions for testing the impact of learning opportunities, neophobia and human exposure during an individual's lifetime. We especially investigated the relationship between human orientation and cognitive performance in physical cognition tasks. The results show that already before extreme enculturation, human orientation among captive great apes predicts their attitude and knowledge about problem-solving tasks, and thus influences within-species variation in performance levels (*chapter 5*).

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Chapter 2

Contrasting Responses to Novelty by Wild and Captive Orangutans

Published in American Journal of Primatology June 2015

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2.1 Abstract

Several studies have suggested that wild primates tend to behave with caution toward novelty, whereas captive primates are thought to be less neophobic, more exploratory and more innovative. However, few studies have systematically compared captive and wild individuals of the same species to document this "*captivity effect*" in greater detail. Here we report the responses of both wild and captive orangutans to the same novel items. Novel objects were presented to wild orangutans on multiple platforms placed in the canopy and equipped with motion-triggered video cameras. The same and different novel objects were also presented to orangutans in two different zoos. The results demonstrate extreme conservatism in both Bornean and Sumatran wild orangutans, who gradually approached the novel objects more closely as they became familiar, but avoided contact with them over many encounters spanning several months. Their zoo-living conspecifics, in contrast, showed an immediate neophilic response. Our results thus confirm the "*captivity effect*". To the various ecological explanations proposed before (reduced risk and increased time and energy balance for captive individuals relative to wild ones), we add the social information hypothesis, which claims that individuals confronted with novel items preferentially rely on social cues whenever possible. This caution toward novelty disappears when human caretakers become additional role models and can also be eroded when all experience with novelty is positive.

2.2 Introduction

In recent years, interest in novelty response has soared because it is generally seen as a major source of behavioral innovations and creativity (Auersperg *et al*., 2011; Greenberg, 1990; Kaufman & Kaufman, 2004; Kaufman *et al*., 2011; Mettke-Hofmann *et al*., 2002; Reader, 2003), which in turn are regarded as a good measure of cognitive abilities (Reader *et al*., 2011; Reader & Laland, 2002). Novelty response is usually described by two main outcomes, neophilia and neophobia, which are generally considered two independent mechanisms (Carter *et al*., 2012; Greenberg, 2003; Greenberg & Mettke-Hofmann, 2001; Hughes, 2007; Mettke-Hofmann *et al*., 2002; Mettke-Hofmann, 2014; Miranda *et al*., 2013; Pisula *et al*., 2012; Russell, 1973; Sabbatini *et al*., 2007). While neophilia refers to the seeking, approaching and exploration of novelty, neophobia refers to avoidance of, reluctance to approach, or even fear of, novelty (Greenberg, 1990; Mettke-Hofmann *et al*., 2006; Mettke-Hofmann, 2014).

The aim of this study was to examine how wild and captive orangutans respond to novel artifacts. Since what is novel is highly context dependent, responses may differ both qualitatively and quantitatively (Heyser & Chemero, 2011; Mettke-Hofmann et al., 2006). Because we could not measure the subjects' internal state (Mettke-Hofmann *et al*., 2006), and thus could not estimate distress and fear, our focus here is on the observable behaviors. Various other studies have also estimated neophilia/ neophobia

as approach rates to novel artifacts and/or willingness to feed near them (Benson-Amram *et al*., 2013; Bergman & Kitchen, 2009; Mettke-Hofmann *et al*., 2002; Webster & Lefebvre, 2001).

In primates, most studies of novelty response conducted on captive groups describe neophilia (Addessi *et al*., 2007; Chamove, 1983; Ehrlich, 1970; Glickman & Sroges, 1966; Joubert & Vauclair, 1986; Visalberghi, 1988). In contrast, the few available studies of wild primates report cautiousness toward novel artifacts (Menzel, 1966; Visalberghi *et al*., 2003). To ensure that this difference reflects the contrast between wild and captive conditions, within-species comparisons are required. We know of only two such comparisons with primates. First, after a habituation phase of banana provisioning on platforms, Visalberghi *et al*. (2003) investigated reactions towards novel food and novel objects in a group of free-ranging capuchin monkeys, *Cebus apella*. In contrast to captive capuchins (Visalberghi, 1988; Visalberghi & Fragaszy, 1995), wild capuchins consumed very little of the novel food presented to them; furthermore they delayed approaching both novel food and novel objects compared to familiar food. A second study, involving rhesus macaques, *Macaca mulatta*, compared captive with semi-free ranging individuals, with similar results (Johnson, 2000). Thus, in contrast to the curiosity and neophilia reported from captivity, among wild primates novelty seems to elicit avoidance. Among non-primates, the only such comparison involves spotted hyenas, *Crocuta crocuta*, again with the same outcome (Benson-Amram *et al*., 2013). Moreover, among primates, there is growing evidence for social influences on the integration of novel food items into feeding repertoires (Addessi *et al*., 2007; Leca *et al*., 2007; Schuppli *et al*., 2012; Ueno & Matsuzawa, 2004; Visalberghi & Addessi, 2000; Visalberghi & Fragaszy, 1995), suggesting that upon encounter with novelty, primates use social cues rather than risky independent exploration.

Other differences between wild and captive primates in the cognitive domain are consistent with differential responses to novelty, although they may also have other causes. Some primate species are known to use tools only in captivity, and some species using tools in the wild only manufacture them in captivity (Haslam, 2013; van Schaik *et al*., 1999). Wild orangutans (*Pongo spp*.), for instance, use a handful of simple tools, such as sticks and leaves, whereas their captive counterparts have a broader tool repertoire, perhaps because human induced artifacts create a broader range of opportunities than possible with naturally occurring objects (Byrne & Russon, 1998; Russon & Galdikas, 1993; Shumaker *et al*., 2011). Moreover, captive baboons, *Papio anubis*, performed better in problem-solving tasks than wild conspecifics (Laidre, 2007), a pattern also confirmed in spotted hyeans (Benson-Amram *et al*., 2013).

This captivity effect has mostly been explained with reference to environmental factors. Reduced predation and foraging pressure provide captive individuals with a risk-free environment, abundant free time, and excess energy (Benson-Amram *et al*., 2013; Haslam, 2013; Kummer & Goodall, 1985, Laidre, 2007). In addition it has been suggested that the exposure to man-made objects reduces

neophobia and enhances object handling (Benson-Amram *et al*., 2013; Laidre, 2007; van de Waal & Bshary, 2010). Further, in some species the social environment also differ in captivity not only resulting in increased social contacts with conspecifics (Haslam, 2013), but also social influence on behavior caused by the ability to attend to humans (Fredman & Whiten, 2008; Hirata *et al*., 2009). It is therefore worth exploring the role of novelty response in the overall cognitive differences between wild and captive conspecifics.

The purpose of this study was to compare the novelty response between wild and zoo-living orangutans in order to examine to what extent we could replicate the "captivity effect" in novelty reactions within this species. We tested novelty responses in two wild populations, one on Sumatra (*Pongo abelii*) and one on Borneo (*Pongo pygmaeus wurmbii*). We also did two different kinds of zoo controls, one in which the exact same items were used and one in which other novel items were used.

2.3 Methods

2.3.1 The wild populations

The experiments on novelty response were conducted on wild orangutans in Indonesia at two study sites: Suaq Balimbing on Sumatra, and Tuanan on Borneo. The study site of Suaq Balimbing is situated in the Kluet region of the Gunung Leuser National Park in the province of Nanggroe Aceh Darussalam (03°39'N, 97°25'E). The Tuanan research site is located in the Mawas Reserve in the Central Kalimantan province (2°09´S, 114°26´E). At Suaq, the experiment was run between November 2010 and April 2011, and at Tuanan between August 2010 and April 2011. During these periods, 28 orangutans were followed as focal subjects and regularily seen in the study area of Suaq Balimbing; eight adult females, two flanged males, four unflanged males, seven adolescents and seven infants. At Tuanan, 28 individuals were regular subjects of focal follows; seven adult females, seven flanged males, two unflanged males, five adolescents and seven infants. The procedures for these experiments were approved by the Department of Forestry and Nature Conservation (PHKA) of the Republic of Indonesia.

During the time period of these experiments we exposed the orangutans in their natural habitat to items they had never encountered before. The novel materials presented were placed upon natural-looking platforms high in the canopy at various sites in the center of the study area, where the home ranges of many known females overlap. Because wild orangutans are occasionally seen exploring old nests in search of insects or re-building them for their own resting purpose, the platforms were established on a rattan base covered with leaves and branches of familiar tree species woven together

to resemble orangutan nests, so the subjects would react toward the novel items rather than the construction itself (Figure 1).

Figure 1: Platforms and novel objects presented to the wild orangutans: A fresh made orangutan night nest, a platform nest made to present the novel objects in the forest, a quadratic red Swiss flag presented together with plastic fruits or plastic flowers, and an orangutan doll.

In Suaq, fifteen such platforms were placed at the most common travel height of orangutans within this habitat, 15- 30 meters (Prasetyo *et al.* , 2009), in four different tree species: *Tetramerista glabra, Horsfieldia polyspherulla, Parastemon urophyllus* and *Sandoricum beccarianum*. The tree species and exact location for the platforms were selected based on ranging patterns and most visited feeding trees, where the orangutans passed by on a regular basis (Figure 2). In Tuanan, where the forest canopy is lower, ten platforms were put up on a height of 10-15 meters in the following species in the center of the study area (Figure 2): *Syzygium sp., Notophoebe umbeliflora, Shorea parvistipulata, Dyera lowii, Neoscortechinia kingii, Sandoricum borneense* and *Payena leerii*.

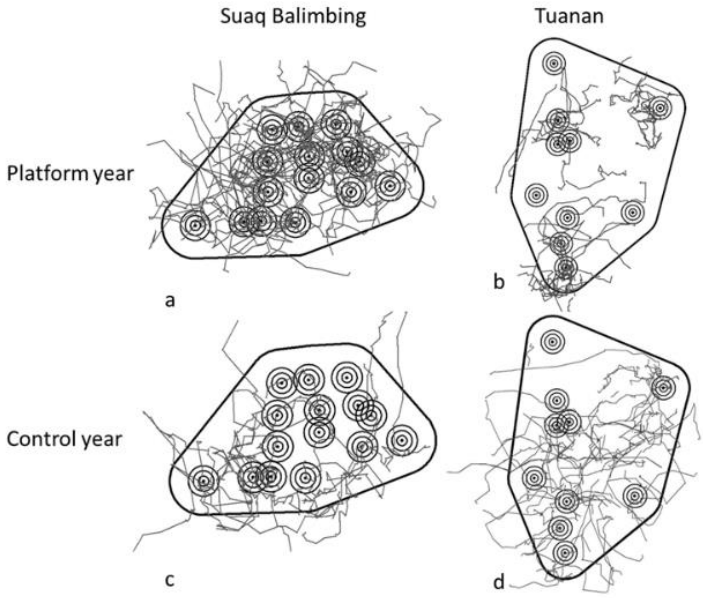

Figure 2: Suaq Balimbing and Tuanan: orangutan travel routes and passes by the platform locations (30 m, 60 m and 90 m) during the experimental time period 2010- 2011 **c** and **d**: Suaq Balimbing and Tuanan: travel routes and passes by the platform locations (no platform) during the control period (Suaq Balimbing: 2013- 2014, Tuanan: 2012- 2013).

The novel objects presented on the platforms were yellow, white or pink plastic flowers, a small red quadratic flag (Swiss) in combination with plastic fruits and a small plush orangutan doll (40 cm)

(Figure 1). Plastic flowers were chosen because their colors stood out against the otherwise green canopy but also might be visually recognized from a distance as a potential food item. Orangutans occasionally feed on flowers from multiple different species familiar to them. The red quadratic flag represented a shape-color combination not naturally occurring in orangutan habitats. It was placed above the platform in order to draw attention to the location and the explorable plastic fruits on the platform below it. The orangutan doll could potentially at a distance resemble an infant sitting on a nest, but at closer proximity perceived as a novel stimulus.

During focal follows at both Suaq Balimbing and Tuanan throughout the experimental period, we recorded all approaches toward a platform within 30 m (the approximate distance at which objects can be seen in the mid-canopy) using standardized focal protocols and ad libitum data (Martin & Bateson, 2007). Focal methods basically followed van Schaik (1999); a complete description can be found at: www.aim.uzh.ch/Research/orangutannetwork.html. At Suaq Balimbing, we additionally recorded all approaches to < 10 m to a platform, gaze direction if at < 10 m and any other responses (when present) of the orangutan. In order to maximize data collection but also to control for human influences on novelty response, five of the fifteen platforms at Suaq Balimbing and four out of ten at Tuanan (one camera less due to technical problems) were equipped with small and inconspicuously placed infra-red-motion-detection video cameras (DVREye Pixcontroller). The cameras were installed to record videos both day and night; batteries lasted up to three weeks, mainly depending on the number of motion-triggered events. The cameras were situated two meters in front of the platform to ensure covering all possible physical interactions on or with the platform.

2.3.2 The captive populations

It may be difficult to compare wild and captive conspecifics, because zoo-living subjects have been exposed to a wide variety of artifacts, making it harder to decide what is truly novel for them rather than merely similar and thus somewhat novel. We thus use the term 'novel' for artifacts never seen before by our subjects and adopted a dual approach. In our first control experiment with a zoo group, we used the same objects that had previously been tested in the wild populations. For the objects used in the wild we chose natural-looking artifacts in order to reduce the degree of novelty, since captive subjects may have more experience with artifacts in general. In an additional experiment on another zoo group, we presented subjects with two novel items of different categories, albeit different from the ones used in the wild, presented in the open. The data collected with the captive populations complied with the Swiss animal protection law and consisted only of non-invasive experiments and behavioral observations in accordance with the principles of the American Society of Primatologists (ASP).

The first control experiment was conducted on seven Sumatran orangutans, *Pongo abelii*, housed in the Zurich Zoo: one unflanged male, one male infant, and five adult females, one of whom experienced

her first pregnancy. The captive subjects were housed in an indoor enclosure of 480 m^3 connected with an outdoor area of 188 m^3. Every morning these orangutans are briefly sent into their sleeping quarters or a smaller room while their enclosure is being cleaned. As the orangutans are let back into their main enclosure, they can encounter enrichment objects such as old footballs, rubber pieces, cardboard boxes and paper sacks, within which food is occasionally hidden. These are provided routinely and the orangutans are very familiar with the cleaning process and the objects normally lying around in their enclosure. In order to keep everything as normal as possible during the experimental observations, in the morning after enclosure cleaning, the zookeeper placed the novel objects on the floor in the middle of the enclosure. The orangutans would enter their enclosure from different sleeping quarters at slightly different angles to the object location, but the objects were detectable from all different perspectives. We performed the novelty experiments during three continuous days in December 2011, presenting one type of novel object each day.

Based upon information by the keepers, this group of subjects had never encountered any of these or similar artifacts before. However, the red quadratic flag was excluded from the captive part of this study, because these zoo orangutans are provided with red rectangular paper sacks on a regular basis, and a red flag would therefore not represent any particular novel shape or item to them, and also was not needed to draw attention in the open enclosure. The experimental time was set to one hour, although in all sessions the experiments were discontinued earlier because the objects had been torn into small pieces. The enclosure was video recorded from two different angles throughout the experimental sessions with two SONY HDV handy cameras. Time to first approach until contact with the objects, exploration spans, defined as durations of the manipulations of the objects and distances to other group members were recorded directly at the test sessions as well as subsequently from the videos. As a control condition we used the video recordings of one morning without any novel objects; the same data were collected on interactions with objects familiar to the orangutans in this zoo. On this randomly picked day the familiar enrichment items were red paper sacks and cardboard boxes.

The second control experiment involved slightly different novel artifacts. It was conducted in February 2009 on seven Sumatran orangutans, *Pongo abelii*, housed in Frankfurt zoo. This group of captive subjects was kept in a 253 m^2 enclosure and consisted of one flanged male, three adult females, two immature males and one immature female. In this data set each subject was tested individually, except for mothers with dependent offspring (the latter would not participate in the test). On any given day, one individual was tested with one novel item in their main sleeping quarter. The following novel artifacts were presented on a small open platform: a soft blue rubber ball (diameter 13.5 cm) normally functioning as a dog toy and an Osram LED light, as a control condition approach latencies towards an empty platform were used. The degree of novelty inevitably differed somewhat between the used artifacts: due to the subjects' previous experience with old footballs, the blue rubber ball might be less

novel to them than the flashlight. All experiments were video recorded and analyzed using Mangold interact 8.

All statistical tests were run in SPSS 19. For the wild population of Suaq we had more detailed data on distances and gaze direction; here we used binary logistic regression to calculate the minimal distance at which gaze directed toward novelty occurred, and thus the platform was noticed by the orangutan. We used Spearman rank correlations to investigate the relationship between approaches to novelty and exposure time. For the zoo population, we used the non-parametric Friedman's test, with additional post hoc analysis (Siegel & Castellan, 1988) in order to correct for multiple comparisons with the same subjects. All the data on the captive study at Zurich zoo was taken by SF and in Frankfurt zoo by DH. The data on the wild populations was taken by SF and NZ, accompanied by well-trained field assistants. All the data used in the analyses from the wild involve distances; these are frequently measured by all field staff in our study and trained with calibrated poles.

2.4 Results

2.4.1 Response to novelty in wild orangutans

At Suaq Balimbing, platforms were maintained for 145 days and at Tuanan for 251 days. We first needed to exclude the possibility that there was something about the platform locations, other than the novel objects per se, that kept the orangutans from approaching them. The tree species itself, in which the novel objects were placed, did not influence the likelihood of approaching a platform ($\chi 2$ (1,6)=8.316, P=0.216, N=71). Furthermore, we used ArcGis and GPS data to compare the range use patterns of the focal orangutans in the area with the platforms during the experimental period to a control period (the following year: Suaq Balimbing 2013- 2014, Tuanan 2012- 2013), when orangutans were followed during the exact same time period (and fruiting season), but in the absence of any platforms or cameras. We calculated the rates at which the orangutans passed the platforms at a distance of < 30 m, < 60 m and < 90 m during the experimental period (Figure 2A and 2B), and repeated exactly the same analysis during the subsequent period, examining the passing of the same locations as where the platforms had been situated (Figure 2C and 2D).

The average passes per focal follow for both study sites, Suaq Balimbing and Tuanan (test- and control period), are plotted in Figure 3. The passing rates of the imaginary circles (30 m, 60 m and 90 m) of the platforms during the control phase were slightly lower, because we had used the observed traffic patterns right before the experimental period to decide on the locations of the platforms in order to maximize the possible approach rate. However, there was no evidence that the imaginary 30 m circles around platforms were avoided (Figure 3). We fitted regression lines to the average rate of passes per

follow as a function of distance from the platform locations to assess whether movement was basically random. If there was avoidance of the closest circles to the platform, the fitted lines would intersect the abscissa at values well below 0. The regression lines approximately pass through the origin and their confidence limits all include zero, as expected when movement was random relative to platform location. Similarly, the observed 30 m points during the experimental period do not lie clearly below the line connecting the origin and the rates observed at 60 and 90 m distance. Because the ranging patterns of the orangutans were random relative to the 30 m circle surrounding the platform, we conclude the orangutans showed neither active avoidance of, nor active attraction to the general area around the platforms during the experimental time period.

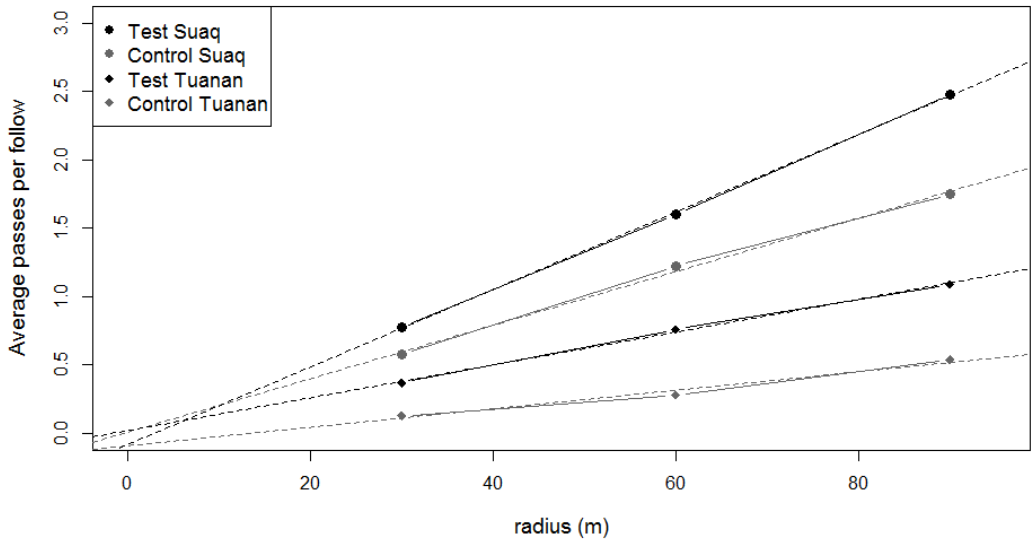

Figure 3: Average passes per full-day follow by wild orangutans at 30, 60 and 90 meters distance from the platform locations during the experimental year 2010- 2011 (test) and during the control periods, when no platforms were present. The straight lines are fitted linear regressions. Note that they all approximately intersect the origin, suggesting no avoidance of the imaginary 30 m circle around the platform.

In the focal follows during the observation period, 59 cases were recorded at Suaq where an orangutan passed the platforms within possible viewing distance (30 m). The number of recorded approaches across the 28 focal followed individuals ranged from 0 to 10. In addition, the motion-triggered video camera traps captured 12 additional independent passes when no human was present (none of which involved physical contact). In total at Suaq 49 approaches to 10 m or closer were noted. At Tuanan, 20 approaches within 30 m were recorded during focal observations, plus none captured on camera (Table I). Because the focal data per individual were too sparse, we used the average pass rate (entering the imaginary 30 m circle) during all focal follows in the experimental period to characterize the average rate for the local population of coming close enough to the novel objects to view them. This rate, as extracted from GPS data in the platform area, was 0.78 per follow for Suaq and 0.37 for Tuanan (Table I). No individuals, apart from two adolescents Shera and Jerry (see below), were recorded to proceed until physical contact with the objects on the platforms during the experimental periods of 145 and 251 days for Suaq and Tuanan.

Table I: Approaches to the platform by wild orangutans at Suaq Balimbing (Sumatra) and Tuanan (Borneo).

Data recorded in the wild populations	Suaq Balimbing	Tuanan
Number of approaches recorded during focal observations	59	20
Number of approaches recorded by video camera trap	12	0
Average passes (<30 m) per follow day	0.78	0.37
Average passes (<60 m) per follow day	1.60	0.76
Average passes (<90 m) per follow day	2.48	1.09
Number of experimental days	145	251
Number of days until first physical interaction with platform	110 (Shera)	74 (Jerry)
Number of focal follows (> 6 hours) in the area during experimental time period	139	311

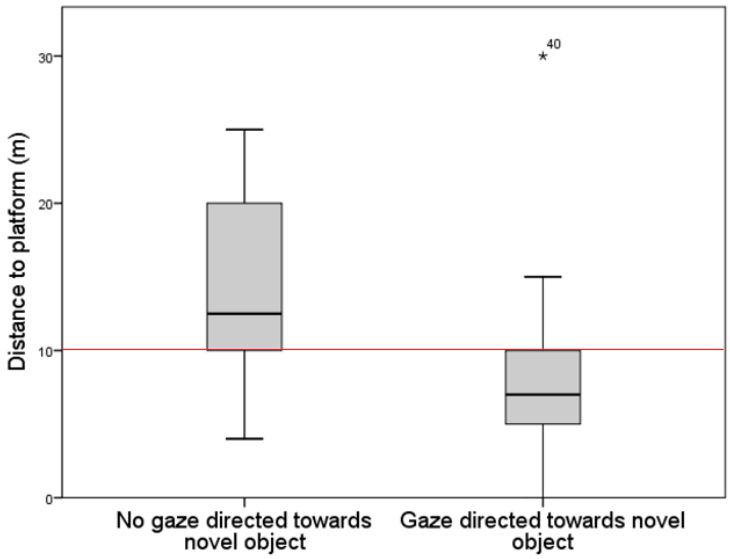

Figure 4: Median distance to platform, provided the focal animal had approached to within 30 meters to the platform, when it did not direct its gaze toward the platform with novel objects (n= 26) versus when it clearly did (n=33).

At Suaq, data was taken on close proximity and gaze direction toward the platforms. At this study site, from 59 recorded approaches to within at least 30 m, 49 were to within 10 m or less. Wild orangutans would direct gaze significantly more toward the platform while they had approached to within 10 m radius than when farther away (binary logistic regression: N=59, Exp (B) =0.861, P=0.006, Figure 4). This implies that at a 10 m distance, the orangutans had usually noted the platform. For all focal follows at Suaq Balimbing we calculated the approach rates (corrected for focal time of each individual) and found that as time went by and the novel objects thus became gradually more familiar, individuals were more likely to approach to within 30 m (Spearman's rho: r=0.260, N=48, P=0.081, Figure 5A). Furthermore, we found that the minimum approach distances, provided there was a close approach to 10 m or less, decreased over time (Spearman's rho: r= -0.439, N=49, P=0.002, Figure 5B). Thus, as time of exposure increased the orangutans gradually approached the objects more closely.

The first and only time a wild orangutan at Suaq made contact with a platform and physically explored its contents was after 110 days. Similarly, at the study site of Tuanan the first and only physical

approach was recorded after the novelty had been presented for 74 days (Table I). The adolescent female that explored the novel objects at Suaq Balimbing (Shera) only approached after her attention had inadvertently been drawn to the platform because she noted a human restoring the platform. After observing the person handling the objects on the platform from a distance, the female approached immediately after the human had climbed down. She moved onto the platform and picked up a plastic red apple and tried to bite in it. After several biting attempts she made a tool out of a small twig and poked at the plastic apple with her twig tool. After unsuccessful attempts with the twig tool she picked up a second red plastic apple and tried a third processing technique by striking it back and forth onto a branch. Shera's manipulation involved a feeding technique frequently used in her population, twig tool use (van Schaik *et al*., 1996). Further, her exploration span resembles the one measured in captive orangutans handling the same objects for the first time (Figure 6). Besides this one approach of physical exploration of the novelty, throughout the same time period at Suaq, 28 cases were recorded during focal follows, where an orangutan would explore a normal old nest, but no cases were seen where an orangutan handled the novel objects. The only individual in Tuanan who approached and physically explored the plastic flowers was a male adolescent (Jerry).

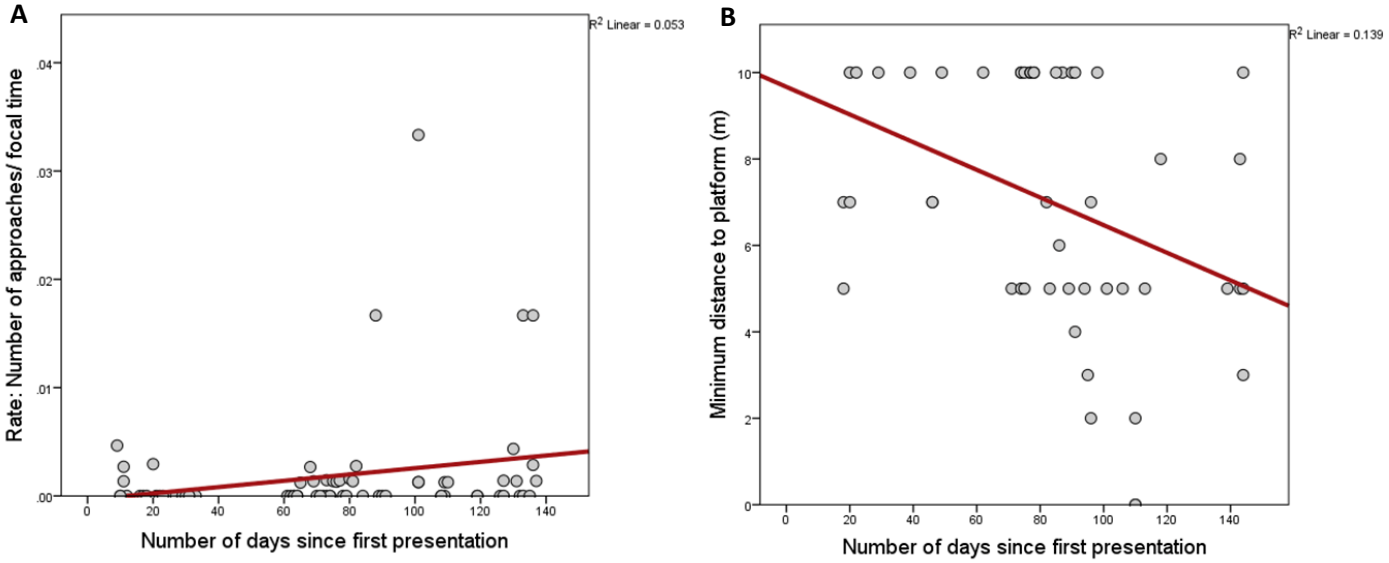

Figure 5. A: Approach rates (number of approaches ≤ 30m per hour focal time) for all individuals with at least five approaches recorded during focal follows as a function of the time elapsed since the novel objects were first presented (exposure time); **B:** Relationship between all close approaches (≤10 m) and exposure time. The data refer to the wild population of orangutans, *Pongo abelii* at Suaq Balimbing.

Both exploring individuals were adolescents. After their exploration of the novel objects no further physical investigation by the same individuals were recorded within the experimental time period. However, Shera passed a second platform with exactly the same objects on the same day only a few hours after she examined the plastic fruits for the first time. The second time around she approached to zero meters of the platform but only visually examined them and did not touch the plastic fruits presented there.

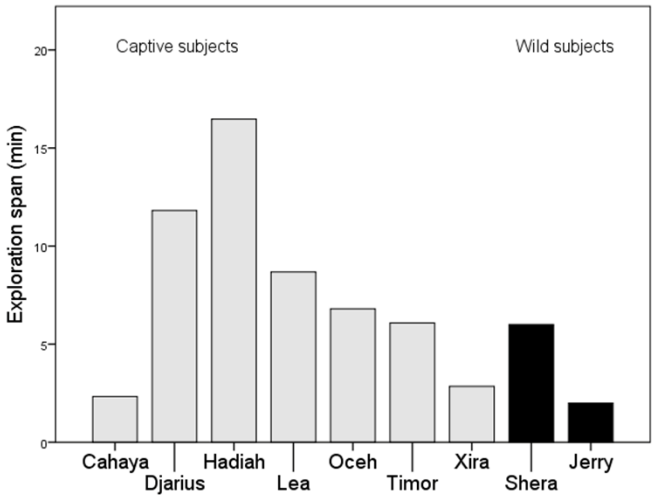

Figure 6: Comparison of exploration spans (in min) between wild (black bars) and captive (gray bars) subjects handling a novel object: a plastic fruit.

Before these first contacts by the adolescents, it is highly unlikely that an orangutan at either site had approached to such close proximity that examination or manipulation of the novel objects would have taken place. First, in five of the 15 platforms at Suaq and four of 10 at Tuanan, such an event would have been recorded by the video camera, because the cameras did capture a diverse range of other animal species visiting the platforms. Second, not a single object was removed or dropped from the platforms, nor did the objects show any bite marks or other signs of physical exploration or disturbance. By using a crude estimate of approaches (mean number of 30 m passes per follow day times experimental days), by the end of the experiment the average orangutan at Suaq Balimbing had passed the platform location approximately 113 times, or 93 times at Tuanan, without ever handling the objects. However, it has to be noted that this estimate is based on the assumption of equal travel patterns for all individuals.

Neither Shera nor Jerry was unusually keen to approach the platforms: 0.44 per follow day (N=16) and 0.25 per follow day (N=8), respectively, close to the average values for their population. Shera's response was similar to that of the population in general, as she too approached the platform to within 30 m more as time went by (approach rate: Spearman's rho r= 0.636, N= 13, P= 0.019) and gradually decreased her approach distance when getting to at least 10 m (Spearman's rho: r= -0.824, N=6, P=0.044). By day 110, when Shera made contact with a platform, we estimate that she had passed by (< 30 m) roughly 48 times. The respective estimate for Jerry at day 74 at Tuanan would be 19 passes. Moreover, another adolescent at Suaq (Ellie) was observed within 10 m to a platform 10 times during the study period, but never physically explored the novel objects.

2.4.2 Response to novelty in captive orangutans

In Zurich zoo the general approach latency towards novel objects was quite different: the Sumatran orangutans approached all novel objects tested within a few minutes (Figure 7A). They had similar approach latencies for the novel objects as for the familiar objects in the control condition (Friedman's test: $\chi 2$ (3)=5.229, N=7, P=0.156). Similarly, the Sumatran orangutans housed in Frankfurt zoo approached the presented novel objects equally fast as the control condition when the platform was empty (Friedman's test: $\chi 2$ (2)=0.519, N7, P= 0.772) (Figure 7A). In both zoo groups approach latencies varied individually, but were similar between the zoos despite the fact that experiments were performed in the group in Zurich and individually in Frankfurt. In the Zurich group the wider distribution of approach latencies toward the novel objects versus the control condition, especially the orangutan doll, was probably caused by the fact that only a single doll was presented in their enclosure. Therefore not all individuals had access to it simultaneously, whereas the familiar objects and the bundles of flowers and fruits could be torn apart for investigation by multiple individuals. In Zurich, because of the dominance hierarchy (S. Lehner, unpublished data), the two older females could not approach while the doll was being monopolized by the adult male.

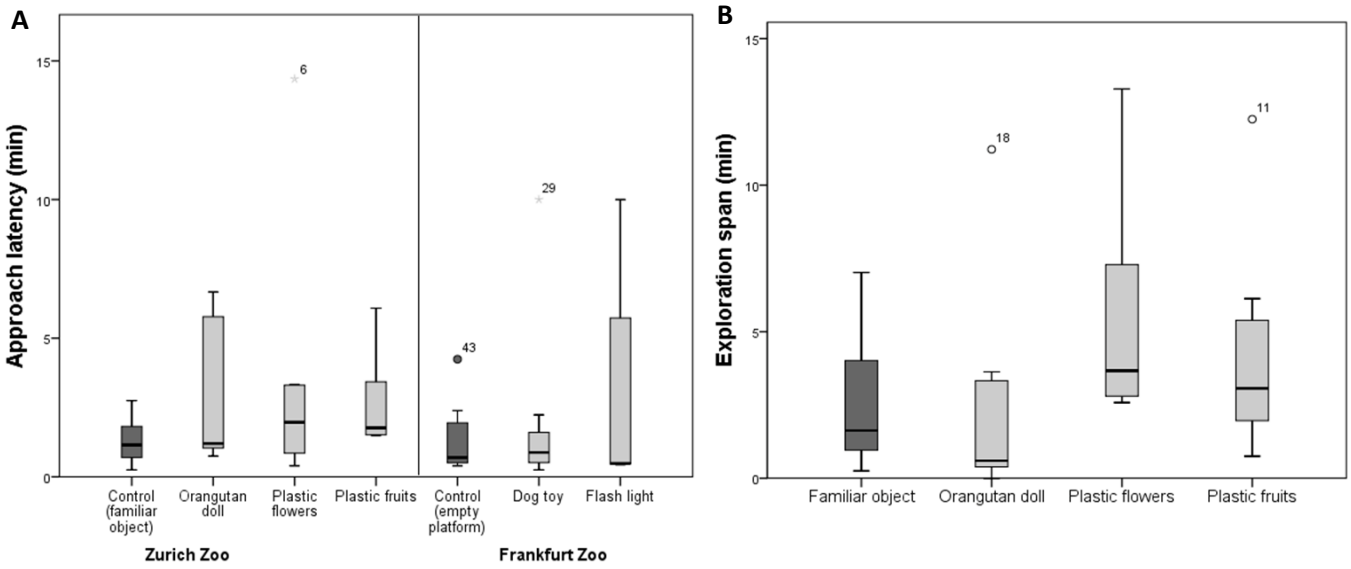

Figure 7. A: Approach to contact latencies (in min) to novel objects by the orangutans in Zurich zoo (the same ones as used for wild orangutans) and in Frankfurt zoo (a blue rubber ball with holes, normally used as a dog toy and a flashlight), compared with those to familiar objects or an empty platform, respectively, serving as a control condition; **B**: Total exploration time in minutes for the orangutans at Zurich zoo handling a familiar object and three novel objects.

In Zurich zoo, where familiar objects served as a control condition, exploration spans were significantly different between conditions (Friedman's test: $\chi 2(3)=8.657$, N=7, P=0.034), but using post hoc analyses and applying a Bonferroni correction, pairwise comparisons revealed that none of the durations between the control condition and the novel objects were significantly different

(between all conditions the critical difference at P=0.05, corrected for multiple comparisons, was 12.74, Figure 7B) (Siegel & Castellan, 1988).

Social proximity during novelty response in Zurich increased during the physical exploration of novel objects. A social partner was significantly more likely to be within two meters when a subject handled one of the novel items than when it was engaging with the familiar paper bags or cardboard boxes (Friedman's test: $\chi 2$ (3)=9.927, N=7, P=0.019, critical difference = 12.74, Figure 8). During this closer proximity individuals often tried to grab the novel item from the individual handling it.

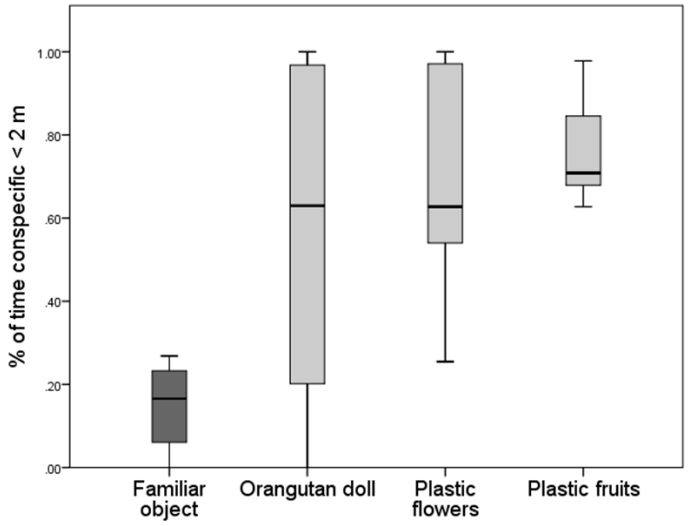

Figure 8: Comparison of close social proximity (< 2 m) when handling a familiar object versus novel objects presented to the orangutans at Zurich zoo.

2.5 Discussion

2.5.1 Wild versus zoo orangutans

Wild orangutans were extremely unresponsive toward the novel artifacts. In fact, the novel objects did not elicit any particular reactions for several months, and therefore we could only report approach data, except for the two cases in which individuals actually handled the novel objects. Although not all platforms were supplemented with cameras, the absence of any physical contact by the orangutans is highly plausible. First, whenever we checked the platforms, the objects showed no signs of having been handled or bitten, and were never found to have been removed. Second, we recorded no contacts during focal follows, except for the two cases of physical interaction (which also left obvious signs of handling on the platforms). Closer approaches were more frequent as time went by (Figure 5A and 5B), and these closer passes were accompanied by visual inspection at a distance, suggesting gradual habituation to the novelty but no approach proceeding to physical exploration of the artificial objects. The two adolescents who eventually responded (one in each population) did so after several months of potential exposure. Indeed, contact latencies amounted to dozens of passes in the wild, even for the two adolescents who made contact after an estimated 48 and 19 passes (the latter necessarily are

estimates, extrapolated from their mean number of passes per follow day). Although the others orangutans had passed the platforms with novel objects at < 30 m about 100 times, they did not make contact with them.

In contrast to their wild counterparts, zoo orangutans approached almost immediately after noticing the novel objects for the first time, regardless of whether they were the same items as used in the wild (Zurich zoo) or other perhaps somewhat more novel objects (Frankfurt zoo), and irrespective of whether they were tested as a group (Zurich) or alone (Frankfurt). Thus, their contact latencies correspond to a single pass in the wild, and contact ensued within a few minutes at most. Zoo orangutans approached all the novel objects as fast as the control conditions of familiar paper sacks and cardboard boxes or an empty platform (Figure 7A and 7B).

In the zoo setting the subjects also spent equal time exploring the novel objects as they did the familiar ones (Figure 7B), suggesting interest in the unfamiliar even though no success in food search followed. Even if the zoo subjects regarded the novel objects as less novel than their wild counterparts, given their previous enrichment experience, they were clearly equally willing to approach and explore the novel objects as the familiar ones. This indicates that these groups of zoo-housed orangutans do not distinguish novel items as irrelevant nor potentially harmful compared to familiar ones.

The comparison, though producing a striking contrast, was not entirely unbiased. First, the animals tested in Zurich zoo were always in association, and it has been shown that association reduces neophobia so that novelty is approached faster in a group context than alone (Marzlufi & Heinrich, 1991; Stöwe *et al*., 2006). However, in the study performed at Frankfurt zoo each subject was tested individually and showed similar short approach latencies. Moreover, the orangutans at Suaq are also frequently in association (van Schaik *et al*., 1999), so differential sociality can only explain a small part of the difference. Second, novelty may cause stronger reactions in a familiar environment (Harris & Knowlton, 2001), and the zoo animals live in far smaller enclosures than their wild counterparts. However, the latter are obviously also very familiar with their habitat, (e.g. Janmaat *et al*., 2012), and continued to show no response toward the novel objects after dozens of passes. Thus, while the comparison cannot be made totally unbiased, the dramatic difference we observed is real and requires explanation.

2.5.2 Explaining the captivity effect

This documented marked difference between wild and zoo orangutans in their response to artificial novel objects suggests that something about these two conditions fundamentally changes the response to novelty. So far, the main explanation has referred to time constraints. Due to the lack of predation

pressure and foraging challenges, captivity has been argued to provide animals with a more relaxed time budget (Kummer & Goodall, 1985) or an excess of energy (Benson-Amram *et al*., 2013), allowing for more exploration. However, Benson-Amram *et al*. (2013) demonstrated that the higher problem-solving ability in captive versus wild spotted hyenas could be attributed to reduced neophobia rather than differences in time and energy. Thus, while the reduced attentional and perceptual load in captivity (due to lack of predation or the need to search for food and plan the daily routes) may free up animals to become more exploratory, having more free time per se does not explain reduced neophobia.

One key factor may well be risk (Haslam, 2013; Kummer & Goodall, 1985). Wild orangutans cannot know whether novel objects are dangerous, and given their long life expectancy (Wich *et al*., 2004) may benefit from being conservative. Because exploration times themselves were similar for zoo and wild orangutans, once the latter approached the items (Figure 7A and 7B), the difference between the wild and captivity is truly in the lack of avoidance of novelty. Risk assessment surely differed between the two conditions. Zoo-living animals only have positive experiences with novel items, which are usually food or playthings, and thus may have overcome any initial neophobia as a consequence of positive reinforcement with man-made objects. In fact given the less diverse environment of a zoo, the zoo subjects may have seen the artifacts as worth approaching and exploring. Their wild counterparts clearly did not. This may appear surprising, given that in the wild especially immature orangutans can spend up to 45 % of their daily activity budget engaged in play, including play with familiar objects in their habitat (van Noordwijk *et al*., 2009). On the other hand, exploration spans were similar between wild and captive subjects once an approach was made. If limited time and energy determined the response, this would not be expected.

While lack of risk and increased value of the objects may cause part of the documented difference between wild and captive orangutans in our study, we also propose social information as a complementary explanation. One obvious way to avoid risk when dealing with novelty is to use social information. Naïve wild orangutans can attend to role models and heavily rely on social learning in the acquisition of their diet. Maturing individuals with abundant opportunities for social learning have come to rely preferentially on socially learned skills to construct their cognitive abilities (*the cultural intelligence hypothesis*: van Schaik & Burkart 2011; see also Herrmann *et al*., 2007; Whiten & van Schaik 2007). They thus follow experienced role models around and minimize independent exploration (e.g. orangutans: Jaeggi *et al*., 2008; Jaeggi *et al*., 2010; van Schaik *et al*., 2003). As a result, naïve orangutans tend not to interact with novel features in their environment until they have seen experienced role models interact with them. Rare food items are more likely to be unfamiliar to these naïve immatures, and indeed in their natural environment, orangutan infants focus much more visual attention toward their mothers when the latter are feeding on food items that are very rare in the feeding repertoire (Jaeggi *et al*., 2010; C.S., unpublished). Interestingly, unfamiliar objects in captivity also elicited social

attention (Figure 8). Thus, the availability of social information is consistent with the novelty avoidance in wild orangutans.

This account suggests that novelty avoidance is the natural response of wild orangutans. The availability of social information can help us understand the loss of novelty avoidance in captivity because in a zoo environment, human keepers serve as additional role models. Once these conditions are in place, the greater opportunity for social learning due to intense contact with conspecifics maintains and even boosts this captivity effect. Thus, we suggest that in species that have the ability to attend to humans as an additional source of information the neophilia seen in captivity arises in part because the novel items (objects, stimuli, and even spaces to some extent) are associated with humans and thus are implicitly approved for exploration. Indeed, semi-free ranging rhesus macaques have been reported to accept novel food faster when handed to them by humans than when they independently discovered it in their habitat (Johnson, 2000). Likewise, orangutan orphans reared in rehabilitation centers and sanctuaries, experience human role models as replacement for their own mothers, and when in semi-natural conditions become very exploratory (Russon *et al*., 2009; Russon *et al*., 2010).

The two cases of contact in the wild are also consistent with a role for social information. When Shera, at Suaq Balimbing, approached and explored the novel objects, her attention had been drawn to them by a familiar human engaging with the objects (note that no physical approach was recorded in the absence of humans by the video camera traps). Furthermore, experiments have shown that infant orangutans refuse novel foods offered by unfamiliar humans unless they witness them being accepted by conspecific adults (Rijksen, 1978). In general the presence of conspecifics influence the acceptance of novel food in orangutans (Gustafsson *et al*., 2014; Hardus, 2012) a pattern also found in some other primate species, e.g. aye-ayes, *Daubentonia* (Krakauer, 2004) and capuchin monkeys, *Cebus apella* (Visalberghi & Addessi, 2000).

Future work should examine the range of species in which the captivity effect can be documented, and moreover what aspects of a captive environment causes novelty response and other behaviors to differ from that in natural habitats. The social information hypothesis predicts that in species with strong orientation toward tolerant role models in regular skill acquisition during development, but also gregarious, tolerant foraging per se, social attendance boosts interest in novelty. However, we stress that this idea is not meant as an alternative to the effects of ecological factors such as limited environmental stimulation, abundant free time and good physical condition. Regardless of the factors causing the captivity effect, an important unresolved question remains to what extent the documented cognitive differences between wild and captive populations (e.g. Laidre 2007; Benson-Amram *et al*., 2013) can be attributed to different attitudes towards novelty.

2.5.3 Neophilia and cognition

Innovations have been shown to correlate with neophilia (Day *et al*., 2003; Webster & Lefebvre, 2001). Wild orangutans avoid novelty. Yet, they have large innovation repertoires (van Schaik *et al*., 2006), and the Sumatran population at Suaq is the technologically most advanced orangutan population, showing a variety of tool uses, which are known to be based on innovations (van Schaik *et al*., 1996; van Schaik, 2004; van Schaik & Knott, 2001). Admittedly, the one individual (Shera) at Suaq exploring a plastic apple used a stick tool to do so, but most others at Suaq ignored these novel objects, also after long exposure time. Moreover, we found no major differences between the Bornean and Sumatran sites with regard to reactions after passing within 30 m of a platform.

This comparison thus supports the idea that novelty response and high innovative ability do not necessarily go together (Brosnan & Hopper, 2014; Griffin & Guez, 2014). First, as noted above, the attitude toward novelty and the tendency to explore are probably independently regulated at the proximate level. There were no differences between the wild and zoo individuals in exploration time, once the latter had proceeded to physical contact with the novel objects. Second, as suggested by the orangutan comparison, highly technologically innovative species, such as great apes, may well owe their large innovation repertoires to their efficient social learning, which strongly increases the chances of persistence of any innovations that happen to have been made (van Schaik *et al*., 2003; see also Koops *et al*., 2014).

2.6 Acknowledgements

We thank following foundations for supporting grants: the Waldemer von Frenckell's foundation, the Paul Schiller foundation, A. H. Schultz foundation, Ella and Georg Ehrnrooths foundation and the International Primatological Society. We especially thank two anonymous reviewers for constructive and valuable comments. We also gratefully acknowledge the following Indonesian institutions for their collaboration and work permissions: the State Ministry of Research and Technology (RISTEK), Universitas Nasional (UNAS), especially Dr. Tatang Mitra Setia and Dr.Sri Suci Utami Atmoko; the Sumatran Orangutan Conservation Programme (SOCP), in particular Dr. Ian Singleton and Santi Delavita Lubis; Yayasan Leuser Ekosistem (YLI); Taman Nasional Gunung Leuser (TNGL), Badan Pengelolaan Kawasan Ekosistem Leuser (BPKEL), MAWAS and the Bornean Orangutan Survival Center in Kalimantan, Direktorat Fasilitasi Organisasi Politik dan Kemasyarakatan, Departamen Dalam Negri, The Department of Forestry and Nature Conservation (PHKA), and the Indonesian Institute of Science (LIPI). We also thank Robert Zingg and the Zurich and Frankfurt Zoo for the effective collaboration.

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Chapter 3

The Paradox of Neophobic Explorers: the Social Information Hypothesis

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3.1 Abstract

It is often thought that innovative species are those that are attracted to novelty. These species would thus benefit from a combination of low neophobia and a high exploration drive, which are known to be independently regulated motivations. Here we draw attention to the innovation paradox: the most innovative vertebrate animals tend to show neophobic reactions when confronted with novel objects or food. Whereas previous work has often stressed the role of ecological factors (dietary flexibility and predation risk), here we also consider the role of social information, especially in species with slow life history. We find that empirical studies support the role of both ecological factors and social information. Specifically, we see that neophobia is generally reduced by social facilitation and the presence of experts. Age effects vary depending on access to social information: where it is present, young individuals can afford to be neophobic, where it is absent or the novelty is classified as non-dangerous, immatures are less neophobic than adults. We draw attention to a strong neophobia-reducing effect of being in captivity, an important cause of which is that humans act as social information sources. We propose that the species showing the paradoxical combination of strong neophobia and strong exploration tendency can rely on social information to select aspects of the environment worth exploring, and also tend to have a slow-paced life history, and thus long potential life expectancy. The social information hypothesis can thus explain the innovation paradox.

3.2 Introduction

Novelty response refers to the way an individual responds to novel stimuli (object, food, context, or environment). It is often categorized as neophobia (avoidance of novelty) or neophilia (attraction to novelty). Here we regard neophobia as a behavioral phenomenon, i.e. the avoidance, indifference or lack of interest in novelty. This focus allows us to remain uncommitted about the underlying motivation; this can be either aversion or fear, but these two can normally not be disentangled without additional experiments (Mettke-Hofmann *et al*., 2006). Such analyses are rarely undertaken and would be especially difficult in the wild. As a result, a focus on the regulatory mechanisms would preclude broad comparative analysis. A neophilic response, in contrast, is defined as attraction towards unfamiliar things or places, accompanied by a strong tendency to explore them.

Neophobia and neophilia are often treated as lying on a single linear scale, for instance as the endpoints of the boldness-shyness continuum in personality studies (e.g., Brown *et al*., 2005; Burns, 2008; Frost *et al*., 2007; Wilson *et al*., 1994; Wilson & Stevens, 2005). However, whenever this has been investigated, neophobia and neophilia were found to be independently regulated motivations (Biondi *et al*., 2010; Carter *et al*., 2012; Greenberg, 2003; Greenberg & Mettke-Hofmann, 2001; Hughes, 2007; Mettke-Hofmann, 2014; Mettke-Hofmann *et al*., 2002; Miranda *et al*., 2013; Pisula *et al*., 2012; Russell,

1973; Sabbatini *et al*., 2007). Accordingly, they are also presumably controlled by different genes (Weisstaub *et al*., 2006). Thus, the absence of neophobia does not automatically imply neophilia; likewise, the absence of neophilia does not necessarily indicate neophobia. In the following, we will therefore consider neophobia and neophilia as distinct, independent traits, and to underscore this, we will from here on refer to neophilia as exploration tendency.

One consequence of considering neophobia and exploration tendency as independent variables is that we can examine how they can be combined. This is shown in Figure 1 (after Greenberg & Mettke-Hofmann, 2001; Mettke-Hofmann, 2014), where for ease of reference each variable is dichotomized into low and high. We can therefore ask which kinds of species or individuals are expected to occupy the space defined by these four combinations. In this review we are especially interested in the paradoxical combination of high neophobia and high exploration tendency.

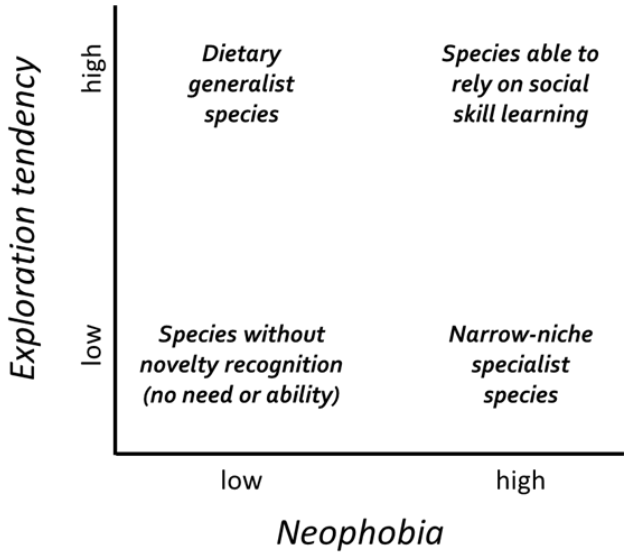

Figure 1: Possible combinations of neophobia and exploration tendency with predicted category of species representing each cell.

Two of the other combinations are straightforward. Dietary generalists, consuming an array of diverse food types, characterized by species with low neophobia and high exploration tendency, have received most attention. They can be contrasted with the opposite combination, characteristic for habitat and diet specialists. The combination of low neophobia and low exploration tendency is unexpected for species that can recognize novelty, because one would expect species with a strong response to novelty to subsequently explore the novel items. This combination is therefore perhaps most likely in species lacking the cognitive abilities to recognize novelty or to gain from exploration, and thus presumably most common among invertebrates. Unfortunately, most research on invertebrate novelty responses concerns spatial neophobia rather than responses to novel objects (Kralj-Fišer & Schuett, 2014), so the generality of novelty recognition in invertebrates remains unexplored. Therefore, in this review we mainly deal with vertebrates, especially birds and mammals.

Our aim is to develop an understanding of the functional basis for the extensive variation in novelty response, especially between species but to some extent also within species. We will do this by developing predictions and then examine the existing studies in light of them. Although the ecological aspects have been much studied and recently been reviewed by Mettke-Hofmann (2014), the non-ecological aspects have so far received less attention, so we will pay particular attention to those.

Because our main focus is on neophobia, we will start by considering its possible functions and by developing predictions. We will next discuss methodological issues potentially influencing the possibility to compare findings on novelty responses. These include the confounding effects of several simultaneous factors that are not always controlled for, individual variation in the perception of novelty and variation in experimental paradigms (Greggor *et al*., 2015). Finally, we assess the predictions with a review of the literature.

3.3 The possible functions of neophobia

Most animals live in habitats where they experience risks such as predation pressure, pathogens, poisonous prey or plant toxins. Thus in many species and conditions there is a benefit to avoiding potentially hazardous novel stimuli, i.e. neophobia (Greenberg & Mettke-Hofmann, 2001). This implies a selective advantage to having such a protection mechanism (Barnett, 1958; Greenberg, 2003; Rozin, 1977). Accordingly, a study of captive-bred swift foxes, *Vulpes velox*, showed how novelty response can affect survival. Individuals with reduced neophobia, as assessed during rearing in captivity, experienced higher mortality than wild-born foxes after release into the wild, suggesting that there are fitness benefits to neophobia (Bremner-Harrison *et al*., 2004).

This functional perspective leads to a basic prediction: animals should avoid novelty if they can (Corey, 1979), but do so less or not at all if they cannot afford to because they lack vital skills or access to resources, or if the risk is so low that it is outweighed by the benefits of exploration (examined below). This basic prediction can be differentiated into many subsidiary predictions, which are all of the ceteris paribus variety, i.e. keeping the effect of other relevant variables constant.

First, animals should be more neophobic if they have access to social information, so they acquire the relevant information without exposing themselves to risk (Galef, 1993). This prediction can be tested both within species (when sociality varies) and between species that vary in sociality. Moreover, individuals that are naïve, either because they are young or recently immigrated, should be especially keen on social information. However, if naïve individuals do not have access to social information or when they are in risk-free contexts, we expect the opposite: they should be less neophobic than adults or residents.

A second subsidiary prediction concerns habitat effects. Where the habitat has intrinsically low risk for the individuals concerned, they are expected to be less neophobic (Greenberg & Mettke-Hofmann, 2001; Brown *et al*., 2013; Mettke-Hofmann, 2014). Such variation may exist within species, e.g. when populations live in different habitats that vary in risk (e.g. urban versus rural), or when captive populations are compared with wild ones. It may also exist between species, e.g. in species living on islands or in highlands without predators versus their close relatives in different habitats. Finally, immigrants entering a new habitat encounter much more novelty and may be forced to be less neophobic than residents, who live in familiar habitats (Martin & Fitzgerald, 2005; Mettke-Hofmann *et al*., 2009; Nilsson *et al*., 2010; Candler & Bernal, 2014). This prediction can apply to individuals or populations of the same species or to different species (for testing purposes ideally congeners).

A third subsidiary prediction concerns the effects of life expectancy on neophobia. Acceptable level of risk should depend on life expectancy (van Schaik *et al*., 2006): where this is low, acceptable risk level goes up and, consequently, neophobia decreases. Thus, old individuals and those that are starving or low-ranking (and thus have lower life expectancy, unless they can improve access to limiting resources) should be less neophobic. Similarly, species with short life expectancies (fast life-history pace) should be less concerned with novelty avoidance than those with long life expectancy. Note that for infants, the life expectancy argument claims that the risk of responding to novelty is highest, whereas their naïve status may imply they have the highest need to do so, unless they have access to social information.

A final prediction concerns the ecological niche. Some species are dietary generalists, and provided they cannot rely on social information, are forced to be less neophobic (Greenberg, 1983; Greenberg, 1984, Greenberg, 1990a; Webster & Lefebvre, 2001). Within species, individuals may vary in personality or genetic endowment. Natural selection may not lead to a single optimum within a population, and individuals may thus differ in the neophobia.

3.3.1 Exploration tendency

Exploration also involves costs, first and foremost because exploring potentially toxic or noxious plant parts and venomous or poisonous prey represent a direct risk. There is also a tradeoff between time dedicated to exploration and other crucial activities, such as attention to predators or hostile conspecifics (Dukas *et al*., 2009). Especially when an explorative act is unsuccessful, e.g. due to limited cognitive abilities, exploration also entails an opportunity cost. Thus, we can make the same basic prediction for exploration as for neophobia. An animal should explore if the risks are minimal and therefore outweighed by alternative strategies such as social learning (O'Hara *et al*., 2012), or if it is dependent on individual exploration in order to gain fundamental skills or access to resources. This

basic prediction can again be differentiated into subsidiary predictions. However, there is far less work that will allow us to test them, in part because in experiments exploration tendency cannot be cleanly separated from novelty response. As a result, we will not examine it in detail here (but see van Schaik *et al*., 2016), but instead mainly emphasize the dependencies between exploration and novelty responses. First, when a species has low neophobia one should also expect a high tendency to explore, since otherwise the response to novelty is not functional. Similarly, a species that lacks a tendency to explore does not need to reduce its neophobia. On the other hand, as we argued above, there may be species that have high neophobia, but nonetheless also have a high tendency to explore.

3.4 Factors affecting comparisons

Reviewing the evidence regarding these numerous predictions concerning novelty response assumes that we can compare existing studies. Apart from lack of control for alternative factors, variation in experimental procedures may hamper comparisons. We therefore must briefly consider methodological issues. When we compare within individuals or between individuals from the same population with the same basic paradigm, novelty responses such as approach latencies and exploratory behaviors should not be affected by the factors we consider below. However, when we compare studies using different paradigms or different species even if using the same paradigm, problems may arise. Although in most published studies such confounding effects are minimized because they assess closely related species, it is important to pay attention to them.

3.4.1 Variation in the recognition of novelty

An obvious precondition for responding to novelty is the ability to recognize novelty per se, in other words, to realize that an object or stimulus, or its context, is different from the familiar one and thus novel (Kaufman *et al*., 2011). Age classes almost certainly vary in their ability to identify novelty, with adults being better than naïve immatures. This variation may be one (usually unacknowledged) source of intraspecific variation. Species may also vary in the ability to recognize novelty, because it requires some minimal cognitive capacity. Studies of hippocampal lesions in rats have shown that novelty response is linked to the size of the hippocampus (Broadbent *et al*., 2004). Similar results are reported for non-human primates in that lesions in the hippocampus impair recognition (Zola & Squire, 2001; Nemanic *et al*., 2004). Thus at least in mammals the hippocampus is involved in novelty recognition (Sokolov, 1963). Although it's relative size varies among animals (Kaufman *et al*., 2011), we are not aware of evidence for variation in the ability to recognize novelty among vertebrates. Major variation is unlikely, however, because insects such as bumblebees, *Bombus terrestris*, can distinguish stimuli of "sameness'" from "difference" (Giurfa *et al*., 2001) and accordingly respond to novelty with avoidance

of the unfamiliar items, followed by exploration before accepting a novel food source (Forrest & Thomson, 2009; Muller *et al*., 2010).

3.4.2 Heterogeneity due to the degree and type of novelty

One source of heterogeneity in responses that is generally not considered is the degree of novelty (Hughes, 1997). Since animals must always compare a new stimulus or context to some standard, the size of the perceived difference from the standard may lead to variation in the strength of the response. Most tests will make the novel stimuli as different as possible to avoid this problem, but if not all studies succeed to an equal extent, this may cause artificial variation in response. This problem may especially affect interspecific comparisons and interpretations on what neophobia tests measure (see extensive discussion by Greggor *et al*., 2015). Furthermore, many studies use human-made objects, which does not necessarily correspond to any novelty an animal may encounter in its natural habitat (see discussion on ecological relevance of novel objects by Koski, 2011).

Once novelty is recognized and assessed, the animal must decide upon a response based on its classification of the novel stimulus as a potential predator or otherwise dangerous object, a potential food item, or a neutral object (Greggor *et al*., 2015) (Figure 2). Moreover, a novel object classified as neutral can be further classified as interesting or not depending on the species' predisposition toward object manipulation or play behavior, which may also depend on age (Koops *et al*., 2015). As a result, novelty responses to different items may vary, and may also be regulated differently (Mettke-Hofmann *et al*., 2006).

These expectations are supported by empirical studies. For example, studies on object exploration in mice, *Mus musculus*, and garden warblers, *Sylvia borin*, have shown that individuals habituate to and approach smaller objects faster than larger objects (Heyser & Chemero, 2011; Mettke-Hofmann *et al*., 2006). Ravens, *Corvus corax*, approached round shaped objects faster than long and thin objects, and novel animal carcasses elicited the longest approach latencies, indicating that the experience of potential predators in the habitat influence the judgment of when to explore (Heinrich *et al*., 1995). Similarly, exploring an unfamiliar space may imply a greater risk than exploring a novel object. In birds (starlings, *Sturnus vulgaris*; mountain chickadees, *Poeclile gambeli*) and fish (guppies, *Poecilia reticulate*), responses to novel surroundings and to novel objects were not correlated, suggesting independent regulation (Boogert *et al*., 2006; Burns, 2008; Fox *et al*., 2009, Carazo *et al*., 2014). Individuals also respond differently to novel stimuli under threatening circumstances (Carter *et al*., 2012). Response to threatening contexts is correlated with neither novel food response (Coleman & Wilson, 1998) nor exploration tendency (Koski & Burkart, 2015; Massen *et al*., 2013, see also Réale *et al*., 2007; Carter *et al*., 2013).

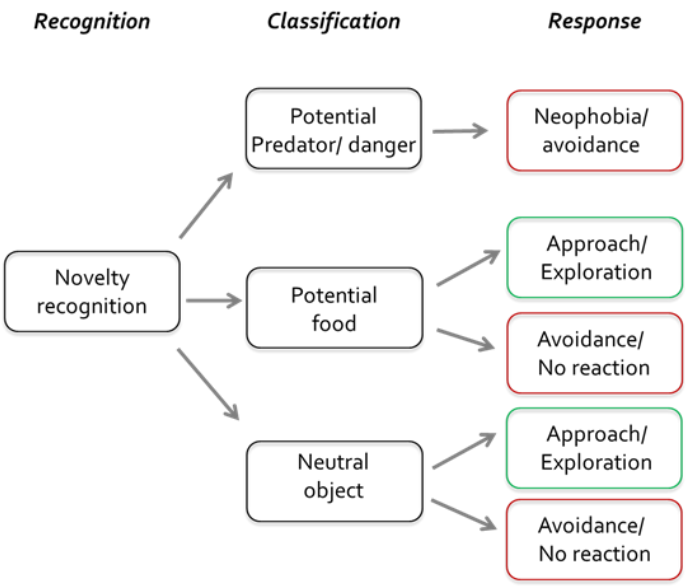

Figure 2: Pathway of possible outcomes of novelty recognition.

In conclusion, different mechanisms may regulate reactions toward novel environments versus novel objects in the environment, or regulate responses to potential food items versus potential predators or poisons. Because of this heterogeneity, we will from here on focus exclusively on novelty reactions toward potentially novel food and novel (non-predatory) objects in general. This choice affects the taxa that we can compare, because most work on invertebrates concerns spatial neophobia (see review: Kralj-Fišer *et al*., 2014).

3.4.3 Heterogeneity due to experimental paradigms

Comparisons between studies may also be hampered by differences in experimental paradigm among studies. Figure 2 shows four major kinds of design: (a) novel objects presented next to familiar food; (b) novel objects per se; (c) novel foods per se; and (d) familiar foods embedded in or associated with novel problem-solving apparatus.

The typical "*neophobia test*" measures approach latencies to a novel object presented next to familiar food or feeding area (Figure 3A) relative to the latency in the absence of the novel object. In the literature this paradigm commonly reports species differences in willingness to feed close to novelty, which might reflect an aspect of risk taking (Greenberg, 1984; Greenberg, 1990; Webster & Lefebvre, 2001; Mettke-Hofmann *et al*., 2002). Variability in the direct approach toward a novel object, also referred to as the "*neophilia test*" (Figure 3B), often captures age or personality differences, so that immature or bold/exploratory individuals tend to show more novel object exploration than adults (Joubert & Vauclair, 1986; Heinrich, 1995b; Mayeaux & Mason, 1998; Bergman & Kitchen, 2009; review of personality literature on boldness: Carter *et al*., 2013). The novel food test (Figure 3C) often reports social influences on approach and acceptance (Addessi *et al*., 2007; Chiarati *et al*., 2012;

Gustafsson *et al*., 2014; Heinrich, 1988; Ueno & Matsuzawa, 2004). A final commonly used design is presentation of a novel problem-solving task or puzzle box containing familiar food (Figure 3D).

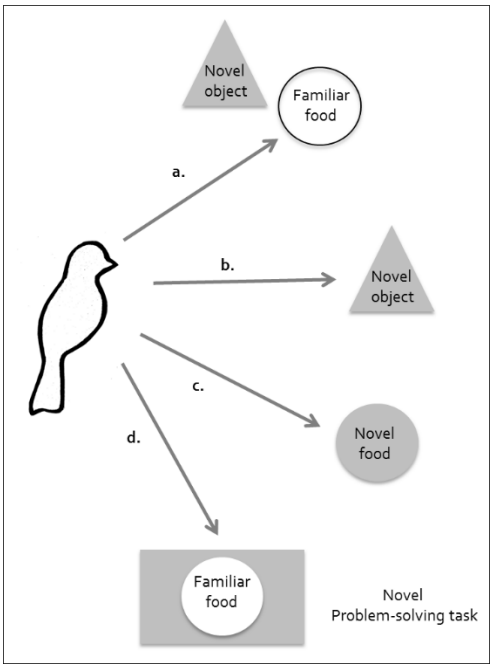

Figure 3: Experimental paradigms commonly used in studies assessing responses toward novelty; **A**. "Neophobia test": a novel object is placed in close proximity to familiar food or foraging site, where approach latency to feed is measured, **B**. Approach latency towards a novel object per se, **C**. Approach and consumption of a novel food item and **D**. A novel foraging task or puzzle-box novel to the animal but presenting a familiar food item as reward.

These studies are mostly designed to measure problem-solving ability or innovativeness. However, from the animal perspective they may be confounded by variation in novelty response elicited by the unfamiliar apparatus. Indeed, some of these studies simultaneously demonstrate a positive relationship between latency to approach the apparatus and success (Auersperg *et al*., 2011; Benson-Amram & Holekamp, 2012; Cauchard *et al*., 2013; Sol *et al*., 2012), whereas others find no link between approach latencies and successful performance (Cole *et al*., 2011; Kendal *et al*., 2005; Shaw *et al*., 2015; Thornton & Samson, 2012). Moreover, in some settings a neophobia test is performed separately from a problem-solving task, but findings regarding the link between the two are diverse: while some studies report a negative relationship between high neophobia scores and problem-solving ability (Biondi *et al*., 2010; Bouchard *et al*., 2007; Koski & Burkart, 2015; Webster & Lefebvre, 2001), others find no influence of neophobia on innovativeness (Boogert *et al*., 2006; Griffin *et al*., 2013; Liker & Bókony, 2009). In conclusion, the kind of study paradigm used may induce variable responses in otherwise identical species or individuals. For example the age effect may be more visible in a novel object test than in a novel food test, simply because youngsters classify neutral objects differently from adults (see age and learning effect below). Thus comparisons, especially between species that are not closely related, should ideally be based on the same paradigm.

In the next sections, we will evaluate the evidence in favor of the various variables affecting neophobia and exploration tendency, in the order indicated in the introduction.

3.5 Social influences on novelty response

A social lifestyle may affect the novelty response of independent individuals in two different ways. First, simply being together with other, equally naïve individuals may reduce the risk of approaching novel objects, because the divided attention needed to attend to the novelty and especially subsequent exploration is less risky when others nearby are vigilant for predators (Dukas *et al*., 2009). Second, naïve individuals, for whom the objects are novel, may rely on experienced individuals, for whom the objects are not novel or are better at classifying it. Accordingly social impacts will be intertwined with age or experience effects. All other things being equal, long association with parents or other caretakers (often linked to slow life-history pace) would favor greater neophobia, because developing individuals can acquire experience through social learning, directly or indirectly. There is indeed evidence for this preferential reliance on social information (Gunst *et al*., 2008; Jaeggi *et al*., 2010; Slagsvold & Wiebe, 2007; van Schaik *et al*., 2016). In contrast, species with non-overlapping generations or a solitary lifestyle will have to be less neophobic than otherwise comparable species that live in association with the parental generation. One such example concerns *Octopus spp*, a taxonomic group reported to respond to novelty in a rather explorative manner (Mather & Anderson, 1999; Oinuma, 2008).

An effect of sociality on neophobia has been reported for a wide range of species (Tables 1-4, Appendix I). Different aspects of social effects are sometimes hard to disentangle. We organized studies according to variability in experimental design, in an attempt to identify the independent effects of sociality per se and of association with experienced individuals. Because age effects and sociality are often intertwined, we also examine intrinsic variation among age-sex classes in novelty response here.

3.5.1 Social facilitation effects

It has often been suggested that a social environment reduces stress when approaching novelty in a group context than exploring alone (Greenberg, 1990a; Moretti *et al*., 2015; Stöwe *et al*., 2006a; Visalberghi & Addessi, 2000). Some studies have focused specifically on testing a possible social facilitation effect by comparing novelty response of the same subjects when they were alone versus when they were in a social context (Table 1, Appendix I). Compared to the solitary condition, a social setting was found to reduce neophobia in tests in various mammals (Forkman, 1991; Moretti *et al*., 2015; Visalberghi & Addessi, 2000; Visalberghi & Fragaszy, 1995; Voelkl *et al*., 2006; Yamamoto & Lopes, 2003) and birds (Coleman & Mellgren, 1994; Soma & Hasegawa, 2004). These studies were all conducted in captive settings where individuals are easily separated for individual testing.

However, when tested in a natural group condition, wild spotted hyenas, *Crocuta crocuta*, also showed significantly shorter approach latencies to a novel problem solving apparatus if a conspecific was already present at the apparatus than when approaching alone (Benson-Amram & Holekamp, 2012).

Some studies did not find social facilitation of the novelty response. In some bird species the social setting did not reduce approach latencies to novelty (Apfelbeck & Raess, 2008; Griffin *et al*., 2013; Overington *et al*., 2009). The negative result in one study could be attributed to details of the experimental design (Apfelbeck & Raess, 2008), but this did not explain the results in other studies. In some cases, birds that are permanently gregarious can afford to have a tendency to simply wait for other, potentially more experienced, individuals to take the lead. This could explain the absence of social facilitation per se in mynahs (Griffin *et al*., 2013; Sol *et al*., 2012), as well as the reports that individuals from larger groups of birds show higher neophobia and higher social tolerance than birds from smaller flocks (Dardenne *et al*., 2013). Alternatively, a negative effect may arise because animals in the social condition are more likely to be scrounged (Bugnyar & Kotrschal, 2002; Coolen & Giraldeau, 2003; Griffin *et al*., 2013; Mathot & Giraldeau, 2010; Stöwe *et al*., 2006a). In conclusion, therefore, a positive effect of sociality on novelty response is commonly, but not universally, found.

3.5.2 Age and learning effects

For a young individual most of the world is novel. We can call this subjective novelty, to stress the fact that the items themselves may have been in the environment for a long time, but are new to the naïve individual. To an experienced adult, in contrast, most of the environment is familiar, and perceived novelty will thus generally be true novelty.

The basic prediction would therefore be that a youngster's neophobia is expected to be lower than that of adults, and its tendency to explore commensurately higher (Figure 4). This prediction holds for solitary species or when risk is regarded very low. However, there may be two conditions in which this prediction may not hold. First, in species in which immatures are reliably accompanied by knowledgeable adults (including parents), the presence of role models during infancy will permit neophobia. However, when immatures and adults are simultaneously exposed to novelty, the immatures may respond more strongly due to social facilitation (discussed above). In either case, we expect immatures to show higher explorative behavior toward items that have been classified as non-dangerous or toward familiar objects than adults.

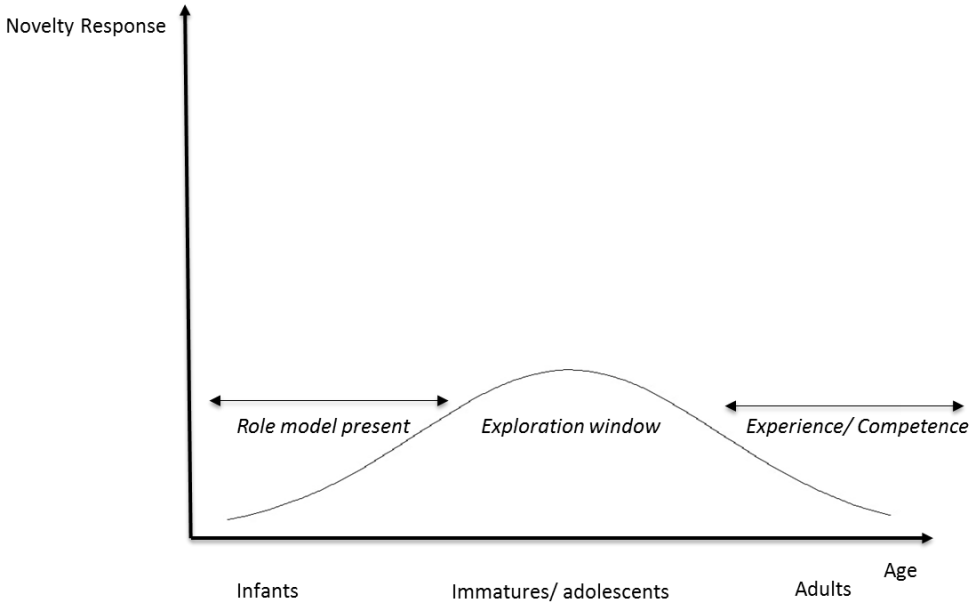

Figure 4: Predicted variation in novelty response during three different life phases (infancy, juvenility + adolescence, and adulthood) of species exhibiting high neophobia and high exploration tendency. During infancy, novelty response must be high when no social information is available, but neophobia is expected where it is. Adolescents often have become independent from parents and other role models, but still benefit from exploration for niche expansion. Under these conditions, neophobia should be reduced and a period of higher independent exploration will ensue. This period comes to an end, once the individual is fully adult and has gained experience to allow it a reduced novelty response.

The second reason for immatures to be more neophobic than adults is linked to life-history pace. For young individuals in species with a slow life history and thus high potential immature survival and long life expectancy, it is unprofitable to jeopardize survival before reproductive age is reached. Therefore they should rely on social information as long as possible. A delay in natal dispersal until well after weaning is believed to be linked to the need to learn vital skills in primates (Deaner *et al*., 2003; Isler & van Schaik, 2009; Schuppli *et al*., 2012), and there is increasing evidence that many birds stay with their parents after fledging (Chiarati *et al*., 2012; Drobniak *et al*., 2015). These conditions should favor higher neophobia in youngsters than adults, especially older adults. This has been argued for humans, where the impact of own mother is strongest in children faced with unfamiliar food (Harper & Sanders, 1975). In many cases, we expect immatures of species with slow life history to rely on social information, and thus be more neophobic than adults, but also nonetheless to be more exploration prone.

Table 2 summarizes the results of experimental studies of this double prediction. They were based on the experimental paradigm of exposing an entire social group to some novel item and compare the age-sex classes in their latency to contact it. The majority of studies listed in Table 2 use the paradigm of Figure 2B: reactions toward a neutral, inedible novel object or a novel problem-solving apparatus. Where a difference is found, immatures, especially the older ones, are more inclined to approach and contact novelty than adults. This may simply due to more experienced adults classifying an object as

irrelevant faster and thus remaining uninterested or losing interest sooner (Figure 4). Indeed the lack of response in adults of both titi monkeys, *Callicebus moloch*, and macaques, *Macaca fuscata*, were reported to reflect indifference rather than caution (Mayeaux & Mason, 1998; Menzel, 1966).

Exceptions may reflect methodological artifacts. While no age effect was reported in wild capuchin monkeys, *Cebus apella*, in response to novel objects, immatures were more responsive towards novel food (Visalberghi *et al*., 2003), which goes against the normal pattern of primates relying on social cues in novel food acceptance (Ueno & Matsuzawa, 2004; Voelkl *et al*., 2006; Yamamoto & Lopes, 2003). The lack of the predicted age pattern here may reflect the fact that the capuchins were habituated to find edible items on platforms (see effect of risk-free habitat below).

It is important to differentiate between infants and juveniles or adolescents. In meerkats, *Suricata suricatta*, juveniles were more likely to approach novelty than adults, whereas pups did not generally interact with the novelty (Thornton & Samson, 2012). This difference between younger infants and other immatures has also been found in other species (Table 2, Appendix I), where the very young ones are more inclined to rely on role models (Biro *et al*., 2003; Fairbanks & McGuire, 1993; Fu *et al*., 2013). The exploration peak during adolescence may be important because it is likely to generate new innovations and thus prevents the erosion of the innovation repertoires of local populations. Overall, then, juveniles and adolescents appear to have the highest tendency to approach novelty.

These conclusions remain tentative, because age-sex classes may differ in their susceptibility to social facilitation. The ideal way to eliminate this possibility is to compare responses between individuals tested alone. Very few studies have done so; they are listed in Table 3. While four studies are consistent with the findings compiled in Table 2, three found that adults had the same motivation to approach novelty as youngsters. It may not be a coincidence that those species are cooperative breeders (Table 3, Appendix I). In species where adults act as caretakers, they may exhibit an intrinsic protective mechanism regarding response to novelty. Obviously, at this stage this remains an open question.

3.5.3 Dependence on experts

In some species individuals might respond differently to knowledgeable experts compared to merely other individuals in their group, or an individual may be especially likely to use social information when there is an asymmetry in knowledge, e.g. in the presence of a trained demonstrator. Table 4 lists the studies on novelty response where some individuals are regarded “experts” and thus the item in the test is not novel to them. All studies found that naive subjects rely on social information when given the opportunity. In birds and rats, naïve individuals learn to avoid unpalatable prey/ food through social learning from more experienced conspecifics (Galef *et al*., 1984; Galef & Wigmore, 1983;

Mason, 1988; Thorogood & Davies, 2012), in part through observation of a conspecific's disgust response (Sherwin *et al*., 2002; Skelhorn, 2011). Even in species not habitually associating with the parental generation, as in many fish, there is evidence that young fish exposed to a demonstrator use social cues in acceptance of novel food (Brown & Laland, 2002). Importantly, these subjects were exposed to a trained or non-trained demonstrator adult fish rather than a group condition, which excludes the social facilitation effect. Thus, we see a widespread effect of asymmetries in social information on novelty response.

The studies compiled in Table 4 also support the idea that the nature of the social cue matters: mothers are preferred over fathers (striped mice, *Rhabdomys pumilio*) (Rymer *et al*., 2008), familiar over unfamiliar (pigs, *Sus domesticus*) (Figueroa *et al*., 2013) and dominant over subordinate (lemurs, *Eulemur macaco macaco*) (Gosset & Roeader, 2001). Reducing risk by trust in a specific social source is implicated by the observation that immature ravens followed a sibling significantly faster towards a novel object than non-siblings even if a social setting per se didn't reduce neophobia (Stöwe *et al*., 2006b). Kin spent more time in close proximity and thus provided more opportunities for both learning and social facilitation (Stöwe *et al*., 2006b). Thus kin may be seen as a more reliable source of social information than non-kin. The same pattern of faster approach in kin-condition was also evident in canids (Table 1, Appendix I) (Moretti *et al*., 2015). A similar pattern holds for primates. Aye-aye infants, *Daubentonia madagascariensis*, accept novel food items only once they had observed their mother consuming them (Krakauer, 2005). Similarly juvenile marmosets, *Callithrix jacchus*, did not consume novel food when tested alone, but did so in the presence of their related adult group members (Yamamoto & Lopes, 2003), although the study did not test whether the same effect was found when tested with non-group member adults.

In addition to the experiments examining social effects on novelty response listed in Table 4, natural observations support the prediction as well. Learning one's feeding niche is closely associated with novelty response, yielding insight into the underlying mechanisms. In various primate species, naïve individuals rely on experienced experts to guide their approach to foods that to them are novel: lemurs, *Eulemur fulvus*, (Tarnaud, 2004), howler monkeys, *Alouatta palliata*, (Whitehead, 1986), mountain gorillas, *Gorilla gorilla beringei*, (Watts, 1985), orangutans, *Pongo spp*, (Jaeggi *et al*., 2008; Schuppli *et al*., 2012), and chimpanzees, *Pan troglodytes* (Lonsdorf, 2006; Matsuzawa *et al*., 2001).

Recent food experiments on great apes showed that social attention to known group members was the main factor influencing ingestion of novel food types also among adults in both chimpanzees and orangutans (Gustafsson *et al*., 2014). Without others present, these species are extremely neophobic in the wild, despite a very opportunistic feeding niche (Forss *et al*., 2015; Takahata *et al*., 1986) (see effect of captivity below). Another study on orangutans exposed to novel food found that repeated exposure to a novel food item did not increase acceptance, but observing a conspecific consuming it

did so (Hardus, 2012). In humans, children are evidently explorative to collect information of their environment, but are nevertheless mostly unenthusiastic when new food is first presented to them. However, this initial food neophobia can be weakened by social influence and multiple experience with unfamiliar food (Addessi *et al*., 2005). Human children in the age of 2-5-years were also able to selectively pay attention whether the demonstrator ate food with same color code as themselves and accepted their novel food accordingly (Addessi *et al*., 2005). Thus the trust in the mother or other tolerant experts is crucial. Overall, therefore, the effect of the presence of trusted experts on immatures' approaching novelty or ingesting novel foods is found in many species.

3.6 The effect of risk variation in different habitats

Some individuals may move between various habitats and thus experience many potential foraging possibilities that are novel to them. Thus, wide-ranging and especially migratory species should show reduced neophobia. Some studies indeed report migrant individuals to be less neophobic than residents in approaching a novel object (Nilsson *et al*., 2010) or in entering a novel room (Mettke-Hofmann *et al*., 2009). Similarly, house sparrows from an expanding population were less neophobic toward novel food when compared with individuals from a long established resident population (Martin & Fitzgerald, 2005). In a migrating warbler species, *Dendroica castanea*, Greenberg (1984) tested reactions to novel and familiar microhabitats and found that the birds preferred foraging in microhabitats resembling those they experienced as juveniles. Thus even if migration and habitat change may reduce neophobia, individuals become more hesitant towards novel habitats as adults by showing a preference for familiarity, consistent with the age effects noted above.

Intriguingly, in between-species context the opposite pattern was found, so that resident bird species are less neophobic and more explorative than migrants. This has been shown in two closely related warbler species, *Sylvia spp*, concerning reactions in a novel space (Mettke-Hofmann, 2007), and in different species of New World blackbirds (*Icterids*), by using the classical neophobia test (Figure 2A) (Mettke-Hofmann *et al*., 2013). These results suggest that at least in these bird genera, migrants are cautious towards potential new risks in an unfamiliar habitat (Mettke-Hofmann *et al*., 2013). However, among the blackbirds the resident species also approached in greater number in the neophobia test, suggesting that social facilitation from conspecifics may have confounded this result.

Nonetheless, these diverse results suggest that additional factors besides habitat may play a role. One possibility is to examine whether young individuals of these particular species acquire their feeding skills through independent exploration or with use of social cues (Lefebvre & Bouchard, 2003; Slagsvold & Wiebe, 2007). Learning a species-specific niche may in fact reveal underlying mechanisms

involved in novelty response. It has also been demonstrated in birds that social learning increases with increasing gregariousness and environmental opportunism (Lefebvre & Giraldeau, 1996).

Another prediction is that where predation risk is generally reduced, species should show reduced neophobia relative to closely related species (Mettke-Hofmann, 2014). In a broad comparison, island species showed shorter latencies to explore novel objects (Mettke-Hofmann *et al*., 2002). This difference may explain why bird species on islands have generally expanded their niches relative to their mainland relatives, and thus the presumed ancestral state (Ebenman & Nilsson, 1982; Yeaton & Cody, 1974). Similarly, living in a safe habitat may explain the increased exploration tendency found in kea parrots, *Nestor notabilis*, living in open, high-altitude habitat (Gajdon *et al*., 2011), and in the robin, *Petroica longipes,* hailing from Kapiti island off New Zeeland (Maloney & McLean, 1995; Shaw *et al*., 2015).

3.6.1 The risk-free existence in captive environments

Individuals may change their novelty response depending on previous experiences or current conditions. For example, individuals living in captive conditions face drastically reduced environmental risks, which modifies the process of an individual's learning about its environment and responses to novelty.

The effect of captivity may have two non-exclusive dimensions. First, reduced neophobia may reflect a repeated lack of negative reinforcement (Haslam, 2013; Kummer & Goodall, 1985). Animals should therefore generally differ between wild and captive conditions. Second, in species attending to role models in their learning processes, human caretakers may become regarded as role models and thus their actions attended to in a similar way. Thus, the captivity effect should be stronger in species that rely on social information, because these species showing the strongest neophobia in the wild.

So far quantitative, systematic comparisons regarding the captivity effect only exist for a few species: wild rats, *Rattus norvegicus* (Barnett, 1958; Tanas & Pisula, 2011), mice, *Mus musculus domesticus* (Kronenberger & Médioni, 1985), hyenas (Benson-Amram, Weldele & Holekamp, 2013), and orangutans (Forss *et al*., 2015). Moreover, strong conservatism toward novelty in the wild, compared to captive conditions have been recorded for primates, which generally rely on social information (Forss *et al*., 2015; Fu *et al*., 2013; Johnson, 2000a; Laidre, 2007; Menzel, 1966; Visalberghi *et al*., 2003). Especially "enculturated" apes can associate human actions with novel objects and attend to them accordingly (Tomasello & Call, 2004; Tomasello *et al*., 1993).

Within-species differences due to rearing and captivity are also reported in birds (see Table 5, Appendix I): ravens, *Corvus corax*, that were reared in captivity approached novel animal carcasses (as well as edible and inedible inanimate novel objects) faster than wild ravens (Heinrich, 1988). Moreover, the captive subjects would approach and interact with any object familiar or non-familiar after the known human experimenter had handled it, supporting the hypothesis that some captive animals beyond primates use their caretakers as sources of social information. Similarly, in orange-winged Amazon parrots, *Amazona amazonica*, hand-reared juveniles were less neophobic than the two other captive treatment groups (parent reared/ human handled and parent reared/ no handling) up until the age of six months. After one year of age all three groups showed same levels of neophobia, which the authors ascribed to the effect of experience the birds had gathered by then (Fox & Millam, 2004). It may not be a coincidence that both reports are for species with slow-paced life history. In other species of birds, captured individuals kept in aviaries may readily respond to both novel objects and foods to participate in learning experiments. This would not be possible with most primates.

We can look more closely at the possible mechanisms underlying the strong reduction of neophobia in captivity in the species that are highly neophobic in the wild. For generalist feeders, it has been argued that food neophobia is acquired after repeated experience of conditioned taste aversion with novel foods (Johnson, 2000b; Rozin, 1976). However, this assumes low or even absent neophobia as the state of departure, which holds neither for these primates nor presumably for many rodents (Barnett, 1958; Galef, 1970; Galef & Clark, 1971). Thus, we should instead look for processes that wear down neophobia. The most obvious candidate is social information: if captive primates consider human caretakers as reliable sources of information, seeing the caretakers handle food and handing it to them should reduce the neophobia toward that food. This habituation and erosion of neophobia towards food offered by humans has been shown in semi-free ranging conditions: macaques accepted novel food faster when it was handed to them from humans than when they encountered the same items in their habitat (Johnson, 2000a). Similarly, baboons, *Papio papio*, responded weakly when tested on novel food-access puzzles in the wild, hardly manipulating the objects used in the experimental set up in order to get to the preferred foods, whereas captive baboons are known to eagerly manipulate objects (Joubert & Vauclair, 1986; Laidre, 2007).

Alternatively, the captive-wild differences have been attributed to time constraints linked to a life in the wild (Kummer & Goodall, 1985), which offers fewer opportunities for developing an understanding about objects and their physical affordances compared to captive life (Laidre, 2007). Nevertheless, wild primates regularly engage in object manipulation within their foraging niche and although time constraints can influence the explorative time devoted to human-introduced objects, they cannot provide the whole explanation for the observed shift in interest towards novelty between captive and wild. Captive individuals may have learned to associate novelty with caregivers and thus allowed this social information to reduce their initial neophobia and induce curiosity. In conclusion, the erosion of

neophobia in captivity can be due to the combination of reduced negative reinforcement and humans acting as social information sources.

Socially encouraged curiosity is well documented in domestic dogs. In a setting associated with humans, dogs, *Canis familiaris*, exhibited prevalence for novel objects when choosing between one novel and two familiar toys (Kaulfuss & Mills, 2008). The process of domestication generally involves selection on reduced neophobia and thus the same two general factors identified above are therefore at work in domestication of dogs as well. First, dogs generally lack negative experiences when approaching and handling novel objects in the presence of humans. Second, dogs are strongly human-oriented and see their owners as trusted experts. Dogs are less neophobic than closely related wolves, even when both are housed in similar captive settings (Moretti *et al*., 2015). Dogs are better at following human actions than wolves, which primarily attend to conspecifics (Range & Virányi, 2014). Thus the domestication of dogs can be seen as an extreme example of the captivity effect.

Reduced neophobia may improve problem-solving ability. In a comparison of captive and wild spotted hyenas, the higher problem-solving ability of captive subjects was attributed to both a reduced neophobia and an increased exploration tendency (Benson-Amram *et al*., 2013). Thus, neophobia, while generally adaptive in the wild, may come at a price, in that the species is less likely to produce sophisticated innovations, and accumulate them through social transmission into cultural repertoires.

3.7 Life expectancy and novelty response

Variation in life-history traits should play a role, in that a long life expectancy will enhance selection on conservatism and risk avoidance, which in turn should also affect the response to novelty. One could expect life expectancy to create interspecific differences in novelty response, but none such broad species comparison exist due to the challenge of controlling for all factors systematically across multiple species. However, within-species differences in novelty response in regard to life history traits are addressed and incorporated in personality studies.

3.7.1 The influence of personality

Studies of animal personalities typically include novelty response as representations of boldness and/or exploration tendency traits (Carter *et al*., 2013; Koski, 2014; Patrick & Weimerskirch, 2014; Wilson *et al*., 1994). Inter-individual variation in novelty responses can arise because optimum behavior depends on physical condition and life history. Individuals with low future prospects of reproduction or survival should increase their fitness potential by taking more risks to maximize energy acquisition and reproduction opportunities. Also, individuals with faster growth rate require more energy and, consequently, take more risks to meet the energy requirements. Conversely, those

with higher likelihood of survival or reproduction, or slower growth, should be more cautious (Biro & Stamps, 2008; Dall *et al*., 2012; Kight *et al*., 2013; Wolf *et al*., 2007). This prediction is supported in the grey mouse lemur, *Microcebus murinus*, where degree of boldness, measured as response to a novel environment as well as a novel object test, is related to life-history trade-offs: younger males with a longer life expectancy and potentially high future reproductive success express lower boldness than older males of the same population (Dammhahn, 2012). Similarly, in domestic dogs, *Canis familiaris*, breeds with more docile or shy behavioral characteristics have lower mortality and lower energy needs than breeds with more aggressive and bold characteristics (Careau *et al*., 2010).

3.7.2 Rank effects

Social status has been suggested to influence novelty responses, but the results are unequivocal. In meerkats, *Suricata suricatta*, subordinate males were less neophobic than dominants towards a new foraging apparatus (Thornton & Samson, 2012), whereas in crows, *Corvus corone*, subordinate birds would overcome neophobia and exploit new food sources only after the dominant male initiated the exploration (Chiarati *et al*., 2012). In coyotes, *Canis latrans*, dominant individuals were also less neophobic than subordinates (Mettler & Shivik, 2007), whereas no clear rank effect was found in wild spotted hyenas, *Crocuta crocuta* (Benson-Amram & Holekamp, 2012) nor capuchin monkey, *Cebus apella*, (Visalberghi *et al*., 2003). These variable findings regarding rank effects indicate that cost and benefits of novelty response may vary in different ways in different social systems, in particular in relation to the skew in access to resources. However, at present, we cannot exclude confounding effects of variable test paradigms.

3.8 Variation due to feeding niche

Dietary effects on neophobia should be widespread. *Ceteris paribus*, one would expect species with a diverse and complex diet to have reduced neophobia in order to maximize use of the feeding niche. Comparing two closely related warbler and sparrow species, Greenberg (1990) experimentally tested for the effect of dietary plasticity and found more specialized species to react with stronger neophobia than their dietary-generalist congeners. Webster and Lefebvre (2001) measured willingness to feed close to a novel object (Figure 3A) to compare *Passeriformes* and *Columbiformes* in their feeding flexibility, but also estimated their responses when faced with novel feeding opportunities in a problem-solving task (Figure 3D). *Passeriformes*, which feed on a broader diet, had shorter approach latencies in the neophobia test and also outperformed the *Columbiformes* in the problem-solving task. However, when comparing two Darwin's finches, Tebbich *et al*., (2012) found that small tree finches, *Camarhynchus parvulus*, show higher neophobia than woodpecker finches, *Cactospiza pallida*, despite

the fact that tree finches forage on a more diverse diet. Thus, diet effects are not clear, perhaps due to uncontrolled confounding variables.

So far the generalist hypothesis has been both developed and largely been tested in birds (Greenberg, 1984; Greenberg, 1990b; Sol *et al*., 2011; Webster & Lefebvre, 2001). Among mammals, however, two related fox species, the culpeo fox, *Pseudalopex culpaeus*, and gray fox, *Pseudalopex griseus*, show the same pattern (Travaini *et al*., 2013). Also, a primate study comparing the sister taxa of wild chacma baboons, *Papio ursinus*, and geladas, *Theropithecus gelada*, showed similar results. Baboons exhibit a more diverse diet and inhibit a broader spectrum of habitat types, and consequently were less neophobic than geladas, which are specialized grazers (Bergman & Kitchen, 2009).

Diversity of habitats may also cause within-species differences. The success of individuals inhabiting urbanized and highly variable habitats are often explained by greater behavioral flexibility, which would predict lowered neophobia compared to conspecifics from stable environments (Sol *et al*., 2011). However, in both woodpecker-, *Cactospiza pallida*, and bullfinches, *Loxigilla barbadensis*, birds experiencing unpredictable habitats showed higher neophobia suggesting that neophobia may not be the underlying mechanism for their expansion success (Audet *et al*., 2015; Tebbich & Teschke, 2014).

Other aspects of feeding ecology have also been suggested to influence neophobia: in a comparison on over sixty parrot species, *Psittacidae*, insectivores showed higher neophobia than folivorous species. To explain this, the authors suggested that ingesting unfamiliar insects can be more dangerous than ingesting unfamiliar leaves (Mettke-Hofmann *et al*., 2002). The same study found that among parrot species, some ecological factors seemed to promote exploration tendencies. Latencies to touch and exploration duration of a novel object did not depend on dietary generalism, but correlated with habitat type (forest edge) and diet composition (buds and fruits). However, because this broad comparative study did not control for other variables, such as life expectancy or sociability, its conclusions should ideally be confirmed.

Extractive foraging is another dietary aspect expected to create variation in exploration tendency (and thus, all other things equal, innovativeness in experimental conditions), especially in primates. Day *et al*., (2003) compared seven *callitrichid* species and found that the more manipulative foraging niche of *Leontopithecus* was correlated with higher exploration tendencies than *Callithrix* and *Saguinus* species. Moreover, being specialized gummivores, *Callithrix* species are extractive foragers and were more explorative than the non-extractive *Saguinus* species.

All these comparisons are affected by the difficulties of disentangling neophobia and exploration tendency in these studies. The ecological hypothesis argues that a species lacking the physiological or

morphological capacity to broaden its diet would not benefit from responding to novel items, and would therefore remain neophobic. Alternatively, however, a species remains neophobic because it would not benefit from exploitation because it lacks the cognitive abilities. So far, this non-exclusive alternative has not been explicitly addressed.

In conclusion, ecological factors such as diet breadth tend to shape novelty response and contribute to species differences. Thus when neophobia is low, foraging plasticity, and so dietary generalism, is achieved through exploration tendency, whereas species inhabiting more restricted niches can afford to be more neophobic (Figure 1). However, given some ambiguities in the various studies, it would be interesting to explore the interaction with social information. In particular, we expect this ecological effect to be most pronounced in species that cannot rely on social information in skill acquisition, or in species experiencing such fast life history or rapid habitat change that social information is unreliable (Giraldeau *et al*., 2002).

3.9 Conclusions

The review suggests that high exploration can be found in conditions characterized by both high and low neophobia (Figure 1). Low neophobia accompanied by high exploration is found where non-risky habitats allow opportunistic, generalist feeders to respond to novelty. Thus the degree of neophobia depends on the costs and benefits of the environment and a species' life-style (generalist vs. specialist, resident vs. migrant and caching vs. non-caching: Mettke-Hofmann, 2014). This combination has long been known for birds and is captured by the generalist hypothesis (Greenberg, 1984; Greenberg, 1990a; Greenberg & Mettke-Hofmann, 2001). It is more likely in species with fast life histories and/or limited access to social information. Similarly, where ecological factors permit suppressed neophobia, especially due to low predation risk, intrinsic exploration tendency rises in species that benefit from opportunistic resource use.

As stressed in this review, however, high exploration can also be accompanied by high neophobia, which is paradoxical and so far somewhat ignored. In these cases, the cause of reduced neophobia is the opportunity to rely on social information rather than ecology. It has often been noted that learning from others is an adaptive strategy in order to avoid potentially dangerous novelty responses (Giraldeau, 1997), especially when it comes to skills rather than perishable information (Rendell *et al*., 2010; van Schaik, 2010). One important finding in the current review was that social information allows a species or individuals to be highly exploratory without simultaneously having to reduce neophobia.

We saw that social information comes in two forms, (i) a more diffuse shared risk form (social facilitation), and (ii) an asymmetric reliance on more knowledgeable, and therefore usually older, experts. The strongest prediction is that species with customary access to social information should show pronounced neophobia, but should subsequently engage in extensive exploration once a social source (expert, role model) has indicated that a particular context is not risky. Moreover, just like risk-free captive habitats, social facilitation and trust in experts allow individuals to explore due to reduced cognitive load as a consequence of reduced vigilance toward predators and other environmental risks. The evidence reviewed here is mostly consistent with these predictions.

The high neophobia-high exploration combination should not just be associated with tolerant sociality but also with slow-paced life history, because both will lead to higher costs of reducing neophobia due to greater opportunities to benefit from social information and their long life expectancy, respectively. This is indeed found in some long-lived species with long parent-offspring associations, often including social access to other tolerant group members: great apes, capuchin monkeys, rhesus macaques, aye-ayes, spotted hyenas and ravens (Addessi *et al*., 2005; Benson-Amram *et al*., 2014; Benson-Amram & Holekamp, 2012; Chiarati *et al*., 2012; Johnson, 2000a). In all these species the default condition of neophobia was reduced in presence of a familiar companion. Similarly, while this conclusion seems warranted, critical tests of the life-history effect, while holding all other effects constant, remain necessary.

A further conclusion worth emphasizing is that novelty response may have coevolved with how young naïve individuals learn their feeding niche. The same underlying psychological mechanisms together with classification ability and relative experience are involved in when and how to avoid potential risk of exploring something new (Figure 4).

It is often predicted that innovative species are species with low neophobia (Auersperg *et al*., 2011; Benson-Amram & Holekamp, 2012; Greenberg, 2003; Sol *et al*., 2002; Webster & Lefebvre, 2001). Given that great apes combine high innovativeness and high neophobia (Biro *et al*., 2003; Boesch, 1995; Manrique *et al*., 2013; van Schaik *et al*., 2006), this link is clearly not universal. There may not have been enough attention to the effects of the novelty-response bias in innovation repertoires in species comparisons. Perhaps the main reason for this lack of concern is that the expected correlations between brain size and innovativeness across species, in both birds and mammals, were found despite these biases (Greenberg & Mettke-Hofmann, 2001; Lefebvre *et al*., 2004; Reader & Laland, 2002). This in turn may have two reasons. First, neophobic species lose their neophobia in captivity, and these species may on average be more innovative. Second, in the wild, the highly neophobic species that rely strongly on social information are exactly those species that acquire most innovations through social learning or by modifying pre-existing behaviors rather than inventing them by responding directly to novelty themselves (Brosnan & Hopper, 2014; Russon *et al*., 2009), which in turn leads to large

standing innovation repertoires in a population. An additional reason is that in species showing highly neophobic behavior, not only social learning but also other cognitive processes are further developed, leading to more effective exploration once neophobia is overcome. Although exploration tendency has been shown to correlate with innovation (Day *et al*., 2003; Greenberg, 2003; Webster & Lefebvre, 2001), one study has reported this relationship to be negative (Kendal *et al*., 2005) and several found no correlation at all (Biondi *et al*., 2010; Mettke-Hofmann *et al*., 2002; Mettke-Hofmann *et al*., 2006). This variability should no longer surprise us.

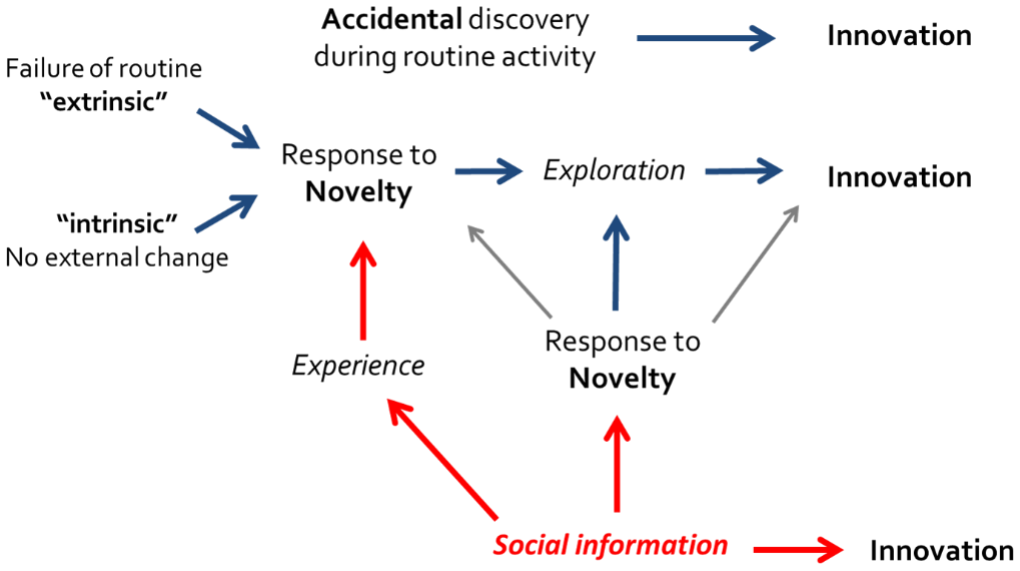

Figure 4: Overview of different innovation pathways.

3.10 Acknowledgements

We are especially grateful to following foundations who have supported funding for this study; A. H. Schultz foundation (Switzerland), Waldemar von Frenckell Foundation (Finland), Ella and Georgh Ehrnrooth Foundation (Finland) and Oskar Öflund Foundation (Finland).

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Chapter 4

Cognitive Differences between Orangutan Species: a Test of the Cultural Intelligence Hypothesis

Published in Scientific Reports July 2016

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4.1 Abstract

Cultural species are able to - or even prefer to - learn their skills from conspecifics. According to the cultural intelligence hypothesis, selection on the underlying mechanisms not only improves this social learning ability but inevitably also the asocial (individual) learning ability. Thus, species with systematically richer opportunities to socially acquire knowledge and skills may over time evolve to become more intelligent, eventually reflected in larger brain size. We experimentally measured problem-solving ability in zoo groups of two closely related great ape species: Sumatran (*Pongo abelii*) and Bornean orangutans (*Pongo pygmaeus*). In the wild, the former is far more sociable than the latter. The homogeneous environmental conditions provided by the nine European zoos allowed us to detect intrinsic differences between the two species. The results on a set of tasks assessing physical cognition revealed an intrinsic species difference in performance, with Sumatrans showing superior problem-solving skills to Borneans, as predicted. The Sumatrans also showed greater inhibitory control and a more cautious and gentle exploration style. The more sociable Sumatran species has therefore experienced stronger selection on the cognitive mechanisms underlying learning.

4.2 Introduction

The cultural intelligence hypothesis (Tomasello, 1995, 1999, 2000) proposes that the capacity of human infants to attend to skills actively demonstrated by experts, was selected for because it is an essential ingredient of our complex ecological niche. Indeed, young children outperform our closest living relatives, the great apes, in socio-cognitive tasks but not in physical cognition tasks (Herrmann *et al*., 2007), indicating that the early-developing socio-cognitive skills serve to scaffold the subsequent construction of physical and spatial cognition. In essence, human intelligence is therefore largely constructed ontogenetically. The core of cultural intelligence is socially mediated learning, defined as the use of social information in the process of acquiring new skills (Heyes, 1994; Heyes & Galef, 1996; Heyes, 2012). Although humans have evolved unique predispositions in both infants and caretakers toward active skill transmission (pedagogy: see Csibra & Gergely, 2011), social learning does occur in other species (Galef & Laland, 2005; Galef, 2006; Laland, 2004) and is instrumental in acquiring both critical ecological (Allen *et al*., 2013; Coelho *et al*., 2015; Esteban *et al*., 2016; Humle *et al*., 2009; Jaeggi *et al*., 2010; Lonsdorf, 2006; Mann & Sargeant, 2003; Perry, 2009; Schuppli *et al*., in prep.) and social skills (Arling & Harlow, 1967; Bloomsmith *et al*., 2006). Moreover, accumulating evidence of geographically distinct traditions has confirmed culture-like phenomena in many non-human animals (Boesch, 1996; Krützen *et al*., 2005; Laland, 2008; McGrew, 1992; van Schaik *et al*., 2003; Whitehead *et al*., 2004, Whiten *et al*., 1999). A broader version of the cultural intelligence hypothesis (Whiten & van Schaik, 2007; van Schaik & Burkart, 2011; cf. Reader & Laland, 2002) therefore focuses on the

quality and quantity of opportunities for social learning as a crucial determinant of culturally constructed intelligence. This version of the cultural intelligence hypothesis has a developmental and an evolutionary dimension (van Schaik & Burkart, 2011). The developmental dimension predicts that the greater the quantity and quality of social inputs experienced by an individual during ontogeny, the more learned skills it can acquire, but also the more experience it can accumulate and thus the better it will be at asocial learning or problem-solving. This process also generates a larger skill pool in a population, which in turn enlarges the individual's set of learned skills (van Schaik & Burkart, 2011).

The evolutionary dimension posits that species with a social system that predictably exposes maturing individuals to numerous opportunities for social learning will be subject to selection on cognitive abilities, whenever fitness is improved by having a larger set of skills, more complex skills, or mastering them earlier in life. Because maturing individuals in such species will routinely accumulate greater experience, they should be more likely to transfer knowledge to other tasks, and thus further improve their ability to solve problems. This process may select for enhanced exploration strategies. Moreover, on longer time scales, such species should also experience selection to enhance the underlying social learning mechanisms. However, due to the cognitive overlap with asocial learning mechanisms (Galef, 1995; Heyes, 1994; Reader, 2003), this selection will indirectly also produce improved asocial learning ability, which over time, will lead to an increase in the innate general cognitive performance in conditions identical to the ancestral state, as well as increased brain size. This broader version should apply to any species that learns socially and maintains this knowledge for generations, although the strength of the effect is likely to depend on the social learning mechanisms and the role played by experts.

To date, although some comparative tests involving brain size were favorable (van Schaik *et al*., 2012), no direct tests of the cognitive predictions of the evolutionary hypothesis have been undertaken. Here we tested the prediction that greater opportunities for social learning are associated with a different exploration style and thus greater asocial learning ability (van Schaik & Burkart, 2011). A systematic comparison of the cognitive abilities of the two orangutan species (*Pongo abelii* on Sumatra, and *Pongo pygmaeus* on Borneo, with an evolutionary divergence estimated from autosomal gene pools of around ~0.9-1.1 Ma) (Greminger, 2015) provides an excellent test of the hypothesis. Orang-utans show extensive social learning during skill development (Jaeggi *et al*., 2010), with more frequent peering and feeding practice as the complexity of foraging skills increases (Schuppli *et al*., 2016). They also show extensive evidence for geographic variation in a variety of skills (Bastian *et al*., 2010; Krützen *et al*., 2011; van Schaik *et al*., 2003; Wich *et al*., 2012). Crucially, Sumatran and Bornean orangutans differ systematically in the frequency of the opportunities for social learning. In similar habitats, Sumatran populations show higher densities (Husson *et al*., 2009; van Schaik *et al*., 1999; Wich *et al*., 2006) and are consistently more gregarious and socially tolerant (Mitra Setia *et al*., 2009; van Schaik *et al*., 1999). They also show much greater repertoires of learned skills and exploratory behavior (Schuppli *et al*.

2016), along with greater cultural repertoires in general (van Schaik *et al*., 2003). This difference in socio-ecology has likely persisted over evolutionary time (Greminger, 2015; van Schaik *et al*., 2009). Note that our choice of species provides a particularly stringent test of the hypothesis because their broadly similar brain size (Taylor & van Schaik, 2007) means that we test the genetic impact of cultural intelligence before pronounced brain size differences have evolved.

Because housing and rearing conditions, ranging from deprivation to enculturation, have a major impact on the cognitive development of apes (Bard & Leavens, 2014; Call & Tomasello, 1996; Russell *et al*., 2011; Tomasello *et al*., 1993; Tomasello & Call, 2004), a proper test of the possibly subtle differences in cognitive performance crucially requires that the conditions be as identical as possible. Since this cannot possibly be achieved in the natural environment, we therefore turned to zoo-housed orangutans. All subjects in this study were mother-reared and zoo-born, and experienced highly similar feeding routines, sleeping quarters, encounters with human keepers and visitors, out-door enclosures and enrichment regimes. In all, 33 subjects in 9 different European zoos were tested on their physical cognitive skills on 4-7 different tasks inspired by the test battery employed by Herrmann *et al*., (2007).

When groups of animals differ in cognitive performance, it is informative to look for underlying differences in their problem-solving strategies, because selection on cognitive performance may actually have targeted these mechanisms. We therefore also tested for the possible role of novelty response, exploration style and inhibitory control, since recent literature has identified these as potentially important mechanisms in conspecific comparisons. First, since cognitive tests inevitably involve some element of novelty, how animals respond to novelty may affect their cognitive performance, as found in several studies (Bouchard *et al*., 2007; Day *et al*., 2003; Seferta *et al*., 2001; Webster & Lefebvre, 2001). Second, exploration styles have been reported to influence cognitive performance. Sometimes, the best problem solvers are the boldest individuals (Dugatkin & Alfieri, 2003; Guillette *et al*., 2009; Trompf & Brown, 2014), at other times, they are the individuals showing frequent and persistent exploration (Benson-Amram & Holekamp, 2012; Huebner & Fichtel, 2015; Kendal *et al*., 2005; Massen *et al*., 2013; Overington *et al*., 2011), whereas in yet other cases, they are those with the most diverse exploratory actions (Griffin *et al*., 2014; Griffin & Guez, 2014). Finally, various studies suggest a relationship between inhibitory control and higher cognitive abilities (Bray *et al*., 2014; Carlson & Moses, 2001; Hauser, 1999; Kralik *et al*., 2002; Manrique *et al*., 2013).

4. 3 Methods

4.3.1 Subjects

We undertook the study in nine European zoos (Table 2, Appendix II), where both species of orangutans are housed under constant and similar conditions, and tested only mother-reared individuals. The European breeding program, EEP, holds all detailed information on birth dates, kinship, transfers and island of origin of all orangutans in European zoos. Table 3 (Appendix II) describes the housing conditions and the time at which the experiments were run at each zoo. All data collected in the United Kingdom were approved by the British and Irish association for zoos and aquariums, BIAZA; all other data were collected in compliance with the Swiss and German animal regulations concerning non-invasive testing on animals.

We presented orangutans of the two species with a set of physical cognition tasks and additionally two tests of novelty response (a novel food and a novel toy) (Figure 1). All subjects participated on their own initiative and individually, which controlled for variation in motivational state between subjects, albeit at the expense of a reduced sample size in some tasks. All tests were conducted either in the morning hours or around mid-day and all subjects were fed normally before and after participating in the tasks. The tasks were presented to the orangutans in their smaller sleeping enclosures or directly in the large home enclosure, whenever a subject could be separated from the rest of the group there. If mothers could not be separated from their dependent offspring, they were tested together with their infants (the latter did not participate in the tasks). Participating subjects ranged in age from five to fifty-two years (Table 4, Appendix II). The average age was 17 years for Sumatran subjects, 21 years for Borneans. All tasks were video recorded with two SONY HDR-CX200 Handy cameras, because to minimize human impacts, no humans were nearby or interacting with the subject during testing.

4.3.2 Description of physical cognition tasks

Inspired by the primate cognition test battery (PCTB) of Herrmann *et al*., (2007) we developed a modified set of physical cognition tasks to assess different aspects of cognition. These tasks were modified because we wanted to make it possible to collect meaningful information without pre-training and frequent interactions with humans, and therefore had to make them as naturalistic and simple as possible, as well as adjust them to different locations of testing.

Detour reaching task

A large transparent plexiglas box (100 cm x 30 cm x 30 cm) was presented in the sleeping enclosure of the subjects. Because the box was placed inside the enclosure it was entirely accessible to the subjects to explore the whole box, providing suitable measurements of explorative actions. Exploratory actions of the plexiglas box were divided into two categories: rough (push, pull, hit) and gentle (touch, poke). The front side of the box had two openings, one small round hole (diameter 2 cm) and one large rectangular opening (30 cm x 20 cm) situated 50 cm from the small opening (Figure 1A). Before the subject entered the test enclosure a food reward (piece of fruit) was placed inside the plexiglas box right behind the small opening, through which the food reward did not fit. The subject would have to prevent its focus on the visible fruit in order to find the large opening and thereby the solution. Each subject was given five minutes to solve this task and the task started as soon as the subject approached to within one meter from the box. The moment the subject touched the fruit piece inside the box was counted as a successful solution and ended the task.

The honey tool-task

This problem-solving task constituted of a wooden box (50 cm x 80 cm x 5 cm) with two traps, which were covered with a plexiglas on the front side for visibility (Figure 1B). The upper trap was a straight, downward-sloping channel (30 cm x 5 cm) filled partly with honey, in which a 40-cm long stick was already inserted (and thus immersed into the honey). The second, lower trap was an L-shaped curve (15 cm x 10 cm), whose interior part, also filled with honey, could not be reached with a finger or a stick. We additionally provided two sticks (40 cm) and three bendable plastic ropes (20 cm) on the floor in front of the apparatus. In order to find the solution for the L-shaped trap, the subject needed to use one of the provided ropes as a tool and dip it into the L-shaped trap. The rope could also be explored as a tool in the straight trap but did not yield any honey reward due to its insufficient length. Likewise, the stick could not reach the honey in the L-shaped trap. The total time a subject was given for this task was ten minutes.

First, we assessed how attentive subjects were toward the test apparatus by calculating the time they spent within one meter of the apparatus as well as the duration of exploration of the apparatus. Exploration was defined as any event were the subject would touch and manipulate any part of the apparatus or the different tools provided right beside the apparatus, minus the time that was spent at performing the solution, e.g. dipping the stick into the straight trap. We also recorded relevant exploration events, which included all exploration events directed toward the two traps and not the apparatus itself (and thus relevant to the actual problem-solving). From this, we calculated the

proportion of total exploration duration during which the subjects focused on relevant exploration. Second, for the cognitive performance we used four measurements from this task:

a) Use of the information provided beforehand: re-use of the stick that was already provided as solution in the straight trap. The stick was counted as re-used if the subject did not let go of it, walked out of sight with it or put it on the floor before re-inserting it into the straight trap. A stick was defined as inserted if at least one third of the stick was inside the straight trap.

b) Correct solution to the straight trap: if the orangutan did at any point during the ten minutes insert the stick to the straight trap, it was defined as a successful solution to the straight trap.

c) Considering the rope as a tool: if the subject did at any point during the ten minutes tried the rope as a tool for either of the traps.

d) Correct solution to the L-shaped trap: if the subject inserted the rope tool into the L-shaped trap during the ten minutes.

The tube-trap task

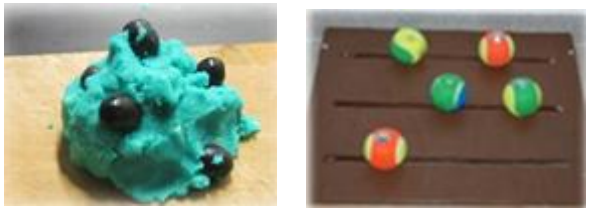
The tube-trap task was also presented to each subject outside of the enclosure mesh, along with sticks to reach six horizontal metal tubes (Figure 1D). Each tube was 30 cm long and 5 cm wide, with an opening on either end, where the stick could be inserted to slide a visible reward (a piece of fruit or a nut) in two different directions. However, the tube had a trap, visible from the outside. Thus, if the reward was moved in the wrong direction it would fall down a 10 cm deep metal cylinder and get trapped. However, if the reward was moved in the correct direction it reached the end of the tube and fell out, to be picked up. The board contained six tubes. Each subject encountered the task in three consecutive trials, resulting in 18 possible attempts. Three tubes had the correct opening on the left side, three on the right side. Thus, if a subject would have a strong side preference and always slide the reward toward one side, it would reach nine correct out of 18 (50%). We therefore calculated the percentage of tubes an individual solved correctly and used a criteria of more than 60% of the tubes correct as a successfully solved task.

Reversal learning task

In this task the orangutans were presented a wooden board, at a distance of ca. 20 cm outside of the enclosure mesh (Figure 1C). The board had 12 holes with 12 lids: six black and six white ones. The subjects were provided sticks to reach the lids of the board. In the first part of the task a food reward (fruit piece or nuts, depending on recommendations or preference of the keepers) was hidden behind either all the black or all the white lids (color was randomly determined for each subject). We determined that the subject had successfully learned the association between right color lid and food

reward once at least five out of the six first lids it touched were of the correct (rewarded) color. In addition, the subject had to pass an extra control trial to ensure it had learned the right association. After the control trial was also successful, we switched the position of the food reward to the opposite color, and counted if and how many trials it took the subject to learn the reverse pattern. The task continued for four days and each subject was given three to four trials per day (depending on when a control trial was needed or not).

A B C D



E F

Figure 1: Set of tasks for testing physical cognition and novelty response. **A**) Detour reaching task **B**) The honey tool-task **C**) Reversal learning board **D**) Tube trap board **E**) Novel Food **F**) Novel toy.

4.3. 3 Novelty response tests

Novel food

As a novel food item we used potato mash that was colored turquoise using regular food coloring and topped with a few black olives (Figure 1E). Each subject was then served a handful of the turquoise potato mash as a little pile on a board right outside the mesh of the test location. The novel food test lasted for a maximum of two minutes, but ended earlier in case all food had already been consumed. We measured the latency to taste the novel food as a proxy for cautiousness. We used the latency of tasting from the point when the subject first touched the item to control for potential differences due to the size of the enclosure mesh through which the subjects had to reach for the food items. As a control condition we also recorded reactions toward a familiar food item, which was either a fruit or vegetable that was part of the subjects' daily diet.

Novel toy

As a novel toy we presented the orangutans with a wooden board containing three slits, in each of which sat two differently colored tennis balls that could be rotated and moved in different directions (Figure 1F). Subjects were given two minutes to interact with the novel toy. Since many zoo-housed

orangutans are familiar with tennis balls (albeit not with these colors or in this context), our intention for this task was to capture how they explore a new task that neither presents any particular problem to be solved nor produces a food reward. Explorative behavior of the toy was divided into the same categories as for the detour reaching task: rough- (bite, hit, pull, push) and gentle exploration (touch, poke, rotate, slide). We calculated exploration rates, counted as number of total exploration events of each category divided by the total time spent with the toy.

4.3.4 Analyses

The same observer (SF) coded all behavior details from the videos of each task using Mangold Interact 9.7. The sample size for each task varied somewhat, because zoos differed slightly in opportunities for separate testing and not all individuals could always be separated. To test for a potential species difference in overall performance (task solved: yes/no), we fitted a Generalized Linear Mixed-effects Model (GLMM) with a binomial error distribution to the data. We incorporated species as the main fixed effect, while task identity, age, sex, group size, and the number of zoos the subject had lived in over the course of its life-time, were included as additional (confounding) fixed effects. Planned contrasts for task (the only categorical predictor with more than two levels) were set to compare a subject's performance on each task to its performance on the detour reaching task (i.e. the task with the highest overall performance, solved by all but 2 subjects). We controlled for repeated observations on each task across the same subjects from different zoos by specifying task identity and individual identity nested within zoo as two crossed random effects. For the exploration data of each task (time to solution) we used standard linear models, with species as independent variable while controlling for age and sex. All statistical analyses were conducted in R version 3.2.3 (Team R Core: 2015), using the "lme4" package (Bates *et al*., 2014).

4.4 Results

4.4.1 Cognitive performance

Overall performance across all 7 tasks was assessed for a total of 33 subjects (14 Bornean, 19 Sumatran) from 9 different zoos. A highly significant binomial GLMM (χ2ML= 33.24, N_{obs}= 196, P< 0.0005; Figure 2, Table 1) revealed that, while controlling for the potentially confounding effects of age, sex, group size, the number of zoos a subject had lived in, and task identity, Sumatran subjects were significantly more likely to solve a task than their Bornean congeners (B= 1.934, SE= 0.74, z= 2.63, P< 0.01). In fact, the odds ratio indicated that the overall odds of a Sumatran subject solving a task were higher as those of a Bornean subject. Our model also reflected that, compared to the detour-reaching task, performance was significantly worse on most other tasks (Table 1). Follow-up models

constructed to investigate the interaction between species and task, failed to converge due to singularities in the Hessian matrix. However, visual inspection of a plot depicting the proportion of subjects within each species that solved each task (Figure 2), suggests that the difference between Sumatran and Bornean individuals was both consistent and of a similar magnitude across all tasks (although possibly more pronounced for the tube trap experiment).

Table 1: Output from the generalized linear mixed model (GLMM) showing species differences in task performance

	B	SE	z value	*P*
Intercept	1.998	1.44		
Species				
Pongo pygmaeus	-	-	-	-
Pongo abelii	1.934	0.74	2.63	**0.0085**
Confounding variables:				
Task				
Detour reaching	-	-	-	-
HT: Straight trap	-1.446	0.97	-1.49	0.1355
HT: Re-use	-4.147	1.06	-3.92	0.0001
HT: Rope tool	-5.258	1.15	-4.58	0.0000
HT: Curved trap	-6.268	1.27	-4.93	0.0000
Reversal learning	-3.441	1.06	-3.26	0.0011
Tube trap: >60%	-4.260	1.12	-3.81	0.0001
Sex				
Female	-	-	-	-
Male	0.448	0.72	0.63	0.5321
Age	0.006	0.03	0.21	0.8306
Number of Zoos	-0.543	0.31	-1.77	0.0774
Group size	0.122	0.12	0.99	0.3235
196 observations on 33 individuals from 9 different zoos, χ^2_{ML}= 86.45, *P*< 0.0001				

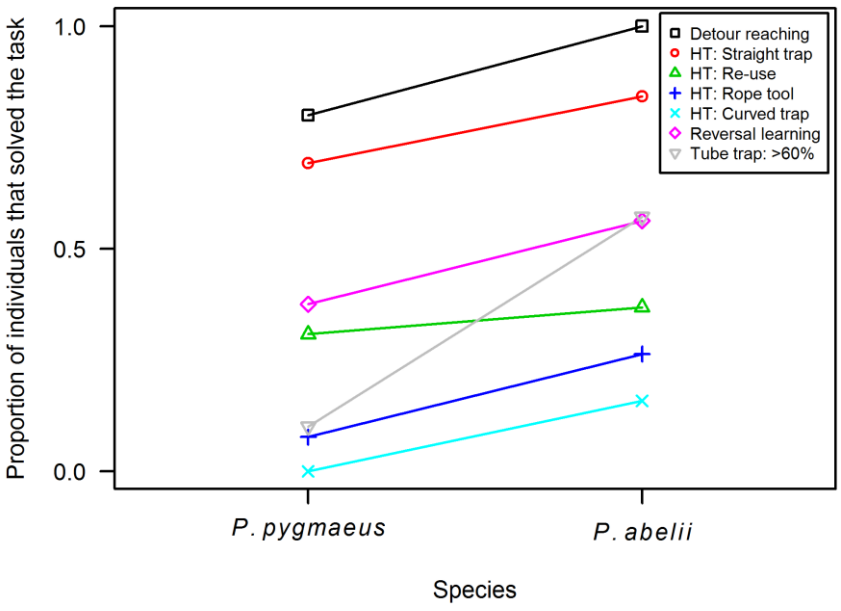


Figure 2: Overall task performance over the different tasks and subtasks between *Pongo pygmaeus* and *Pongo abelii.*

The differences between Sumatran and Bornean subjects actually held across individual tasks and subtasks, even though they were not always significant and we could not control for all the confounding variables in these comparisons. The detour-reaching task lasted for a maximum of five minutes and ended once a subject found the solution. Data on latency to solution and exploration behavior was log transformed in order to fit normally distributed residuals. Our results showed that among successful solvers, Sumatran subjects were significantly faster in solving this problem (LM: $N_{Sumatra}$=10, N_{Borneo}=10, $P_{species}$=0.049, $\beta_{species}$=-94.53±44.28, P_{age}=0.155, P_{sex}=0.760; Figure 3).

In the honey tool-task, Sumatrans were somewhat more likely to solve the stick solution, but the difference in latencies was not significant (LM: $N_{Sumatra}$=19, N_{Borneo}=13, $P_{species}$=0.159, P_{age}=0.143, P_{sex}=0.826). The three individuals who managed to solve the more difficult task of using the rope for the curved trap were all Sumatran.

Because the tube trap task was designed with equally many tubes providing the correct solution toward left respective right side, a subject with a strong side preference for one side would reach 50 percentage correct solved tubes due to its side preference. Thus in order to solve tubes correctly in this task an individual had to suppress any existing side preference and instead decide in each instant toward which side to move the food item. We therefore first looked for the existence of a side preference and found that Sumatrans and Borneans did not differ significantly in the tendency to have a side preference: 70% for Borneans and 85.7% for Sumatrans (Chi-square test: $N_{Sumatra}$=14, N_{Borneo}=10, $\chi2$=2.33, P=0.311). When comparing the number of tubes solved correctly, relative to how many tubes a subject attempted to solve, we found that Sumatran individuals achieved significantly more correct tubes than Borneans (LM: $N_{Sumatra}$=14, N_{Borneo}=8, $P_{species}$=0.011, βspecies=0.127±0.045, P_{age}=0.123, P_{sex}=0.737; Figure 4).

In the reversal learning task all individuals in our sample, both Bornean and Sumatran learned the first association between lid color and food reward. Further, 37.5 percentage of the Bornean subjects and 56.3 percentage of Sumatran learned the reverse color association (Chi-square test: $N_{Sumatra}$=16, N_{Borneo}=8, $\chi2$=0.230, P=0.891), which did not amount to a significant difference.

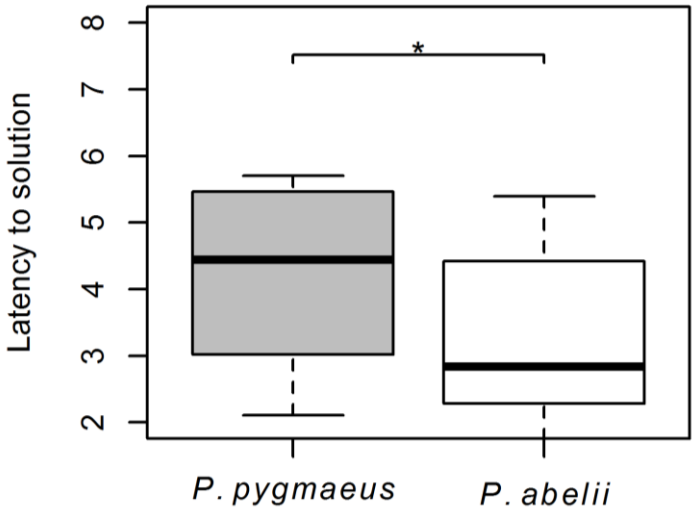


Figure 3: Latency until solution in detour reaching task for both species.

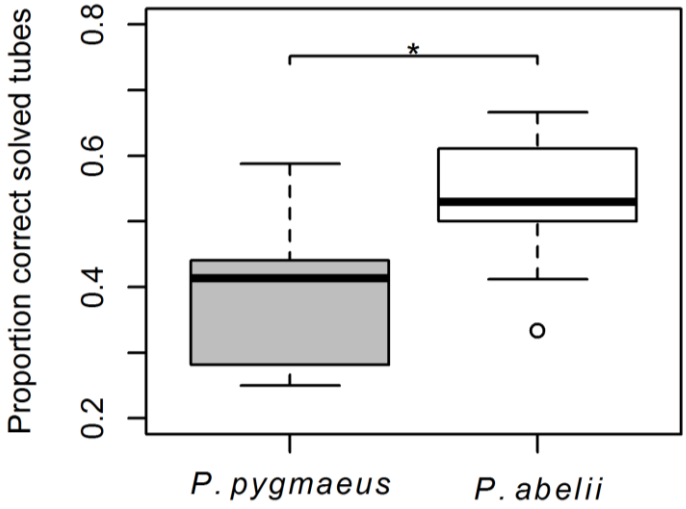


Figure 4: Proportion correctly solved tubes in tube trap task, corrected for total amount of tubes attempted.

4.4.2 Task exploration

We also examined possible mechanisms that could underlie the species difference in cognitive performance, focusing on the latency to ingest novel food, the exploration during tasks as well as of a novel toy, and an assessment of inhibitory control.

Novel food reactions

We compared the two species in their response towards novel food, using their reactions to a familiar food item as the control condition. Data of the response variable (latency to taste novel food) was log transferred in order to reach evenly distributed residuals. We found that the Sumatran species took significantly longer before ingesting the new food than Bornean, but that this was driven by an interaction effect between age and species in the Sumatran sample: (LM: $N_{Sumatra}$=19, N_{Borneo}=12, $P_{species}$<0.001, βspecies=2.179±0.433, P_{sex}=0.726, P_{age}=0.686, $P_{interaction: age/species}$=0.001, $\beta_{interaction: age/species}$ =-0.071±0.018; Figure 5A and 5B). Relative to the Bornean sample, our Sumatran sample contained more young individuals who responded with longer delays to try the novel food. To exclude the fact that those young individuals drove the results of novel food reaction, we also ran the same model excluding all individuals younger than six years. We still obtained the same species difference (LM: $N_{Sumatra}$=14, N_{Borneo}=12, $P_{species}$<0.001, $\beta_{species}$=2.123±0.496, P_{sex}=0.990, P_{age}=0.781, $P_{interaction: age/species}$=0.001, βinteraction: age/species =-0.069±0.020). In the familiar food condition, we found neither a species nor an age effect (LM: $N_{Sumatra}$=15, N_{Borneo}=9, $P_{species}$=0.340, P_{sex}=0.500, P_{age}=0.257; Figure 5C and 5D).

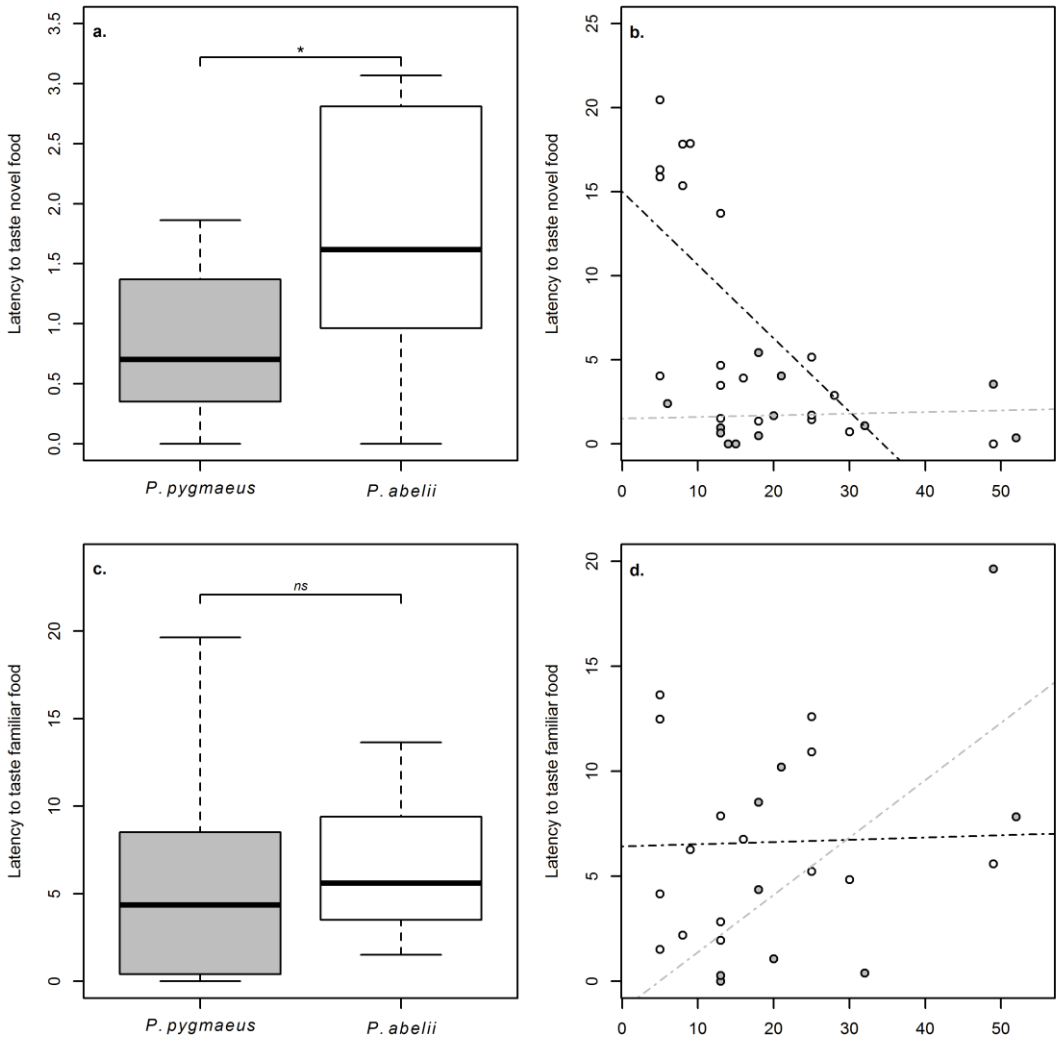


Figure 5: Latencies to taste novel (**A** and **B**) and familiar food (**C** and **D**).

Exploration styles

We also found species differences in the exploration of a novel toy. Compared with Sumatran-, Bornean orangutans showed both higher gentle exploration rates toward novelty (LM: $N_{Sumatra}$=19, N_{Borneo}=9, $P_{species}$=0.031, $\beta_{species}$=-0.163±0.071, P_{age}=0.069, P_{sex}=0.169; Figure 6A) and (especially) higher rough exploration rates (LM: $N_{Sumatra}$=19, N_{Borneo}=9, $P_{species}$<0.001, $\beta_{species}$=-0.167±0.036, P_{age}=0.636, P_{sex}=0.155; Figure 6B).

The same species difference in explorative behavior found in the novel toy test also appeared in the detour-reaching task. Bornean subjects showed significantly more rough exploration (controlled for time at apparatus) than Sumatran (LM: $N_{Sumatra}$=10, N_{Borneo}=10, $P_{species}$=0.042, $\beta_{species}$=-0.050±0.023, P_{age}=0.301, P_{sex}=0.134; Figure 6D). We did not find the same effect when comparing gentle exploration (LM: $N_{Sumatra}$=10, N_{Borneo}=10, $P_{species}$=0.648, P_{age}=0.794, P_{sex}=0.478; Figure 6C).

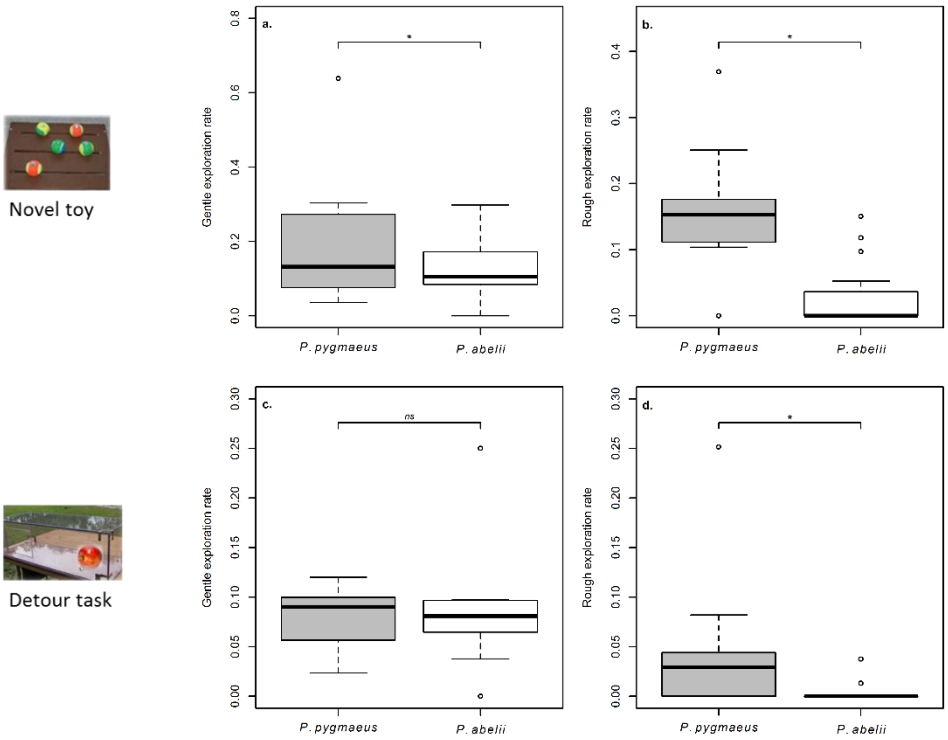


Figure 6: Exploration rates (corrected for total time at apparatus): gentle exploration and rough exploration for both novel toy manipulation (**A** and **B**) and detour reaching task (**C** and **D**).

In the honey tool-task, each subject was given ten minutes time to engage with the apparatus in order to extract honey by choice of right tool for two different traps; straight and curved trap. There was no species difference in either the attentive time (LM: $N_{Sumatra}$=19, N_{Borneo}=13, $P_{species}$=0.903, P_{age}=0.064, P_{sex}=0.811, Figure 7A), or the duration of exploration in this task (LM: $N_{Sumatra}$=19, N_{Borneo}=13, $P_{species}$=0.398, P_{age}=0.094, P_{sex}=0.449, Figure 7B), indicating that individuals of both species were equally motivated to engage with the task. They also did not differ in the variety of exploration acts (LM: $N_{Sumatra}$=19, N_{Borneo}=13, $P_{species}$=0.930, P_{age}=0.465, P_{sex}=0.523, Figure 7C). However, we found a

clear trend that Sumatrans showed higher relevant exploration time compared to Borneans, and that males spent less time on relevant exploration than females (LM: $N_{Sumatra}$=19, N_{Borneo}=13, $P_{species}$=0.064, $\beta_{species}$=0.139±0.072, P_{age}=0.210, P_{sex}=0.029, β_{sex} =-0.183±0.080; Figure 8).

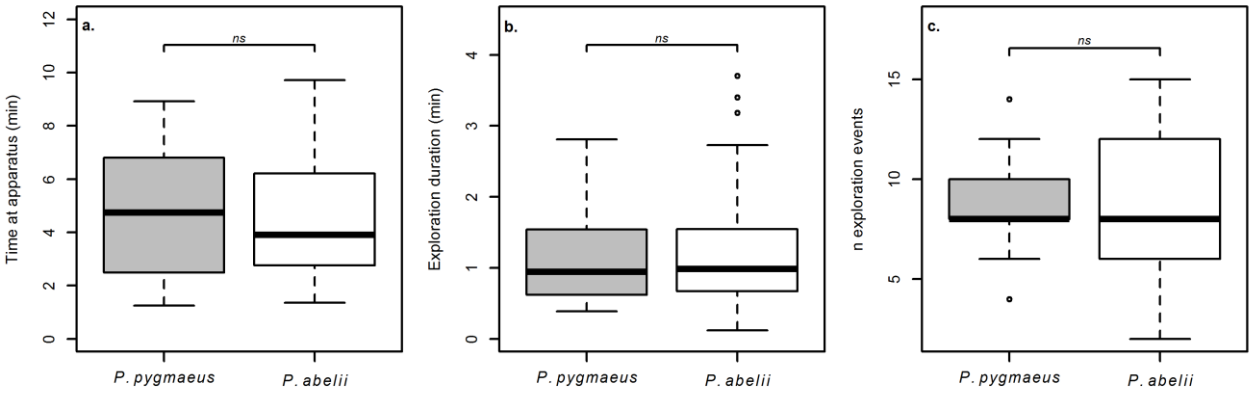


Figure 7: Time spent at the honey tool-task (**A**) and exploration duration during task participation (**B**) as well as the variety of exploration acts used (**C**).

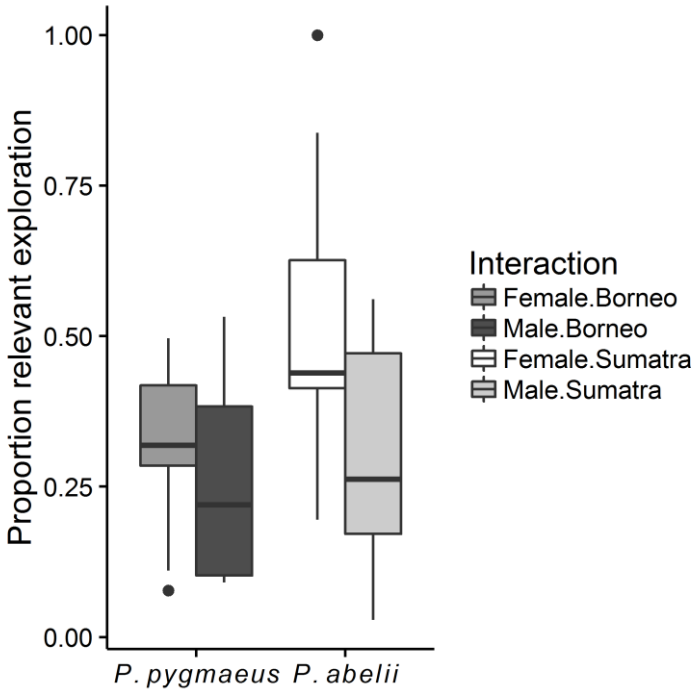


Figure 8: Proportion of relevant exploration time devoted to the honey extraction, corrected for total exploration duration of apparatus.

Inhibition

The reversal learning task provides the opportunity to examine inhibition. When an individual opens the correct lids it acquires information about the specific color and presence of a food reward; equally, opening the wrong lids produces information about the absence of a food reward associated with that color. Once the individual has learned where the food is hidden it should therefore inhibit the tendency

to open the wrong lids. We calculated the total number of lids each subject touched and the proportion of which were of the wrong color and log transferred our data to produce evenly distributed residuals. We found a significant difference between the species: Bornean orangutans opened more of the wrong colored lids than did Sumatran, (LM: $N_{Sumatra}$=16, N_{Borneo}=8, $P_{species}$=0.011, $\beta_{species}$=-0.092±0.033, P_{age}=0.899, P_{sex}=0.475; Figure 9).

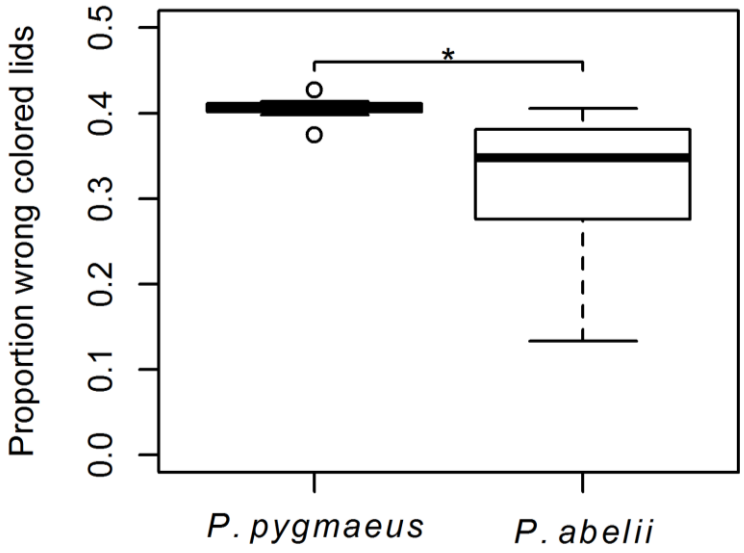


Figure 9: Proportion of lids opened of wrong color corrected for total amount of lids touched in the reversal learning task.

4.5 Discussion

The results showed a clear and consistent pattern: Sumatran orang-utans, *Pongo abelii,* performed better in a variety of tests of physical cognition compared to the Bornean species, *Pongo pygmaeus* (Figure 2 & Table 1). In fact, there was not a single task in which Bornean subjects were more likely to solve the problem than the Sumatrans. The results of the GLMM reveal that variation in cognitive performance was strongly determined by species and revealed no significant effect of group size, age, sex, or the identity of the zoo in which they were kept. Moreover, in the detour-reaching task Sumatran orang-utans were faster at achieving the solution, which required inhibition of fixation on the visible food reward (Figure 3). In the tube-trap task no subject manage to solve more than 12 tubes out of 18, perhaps because most individuals had a side preference, which would have to be suppressed in order to reach a high task performance. Nonetheless, Sumatran orang-utans managed to solve more tubes correctly than the Borneans (Figure 4). These results therefore support the existence of an intrinsic species difference in the ability to solve physical cognition tasks, in agreement with the prediction of the evolutionary version of the cultural intelligence hypothesis.

Given this clear difference in performance on tasks of physical cognition between these two closely related species, it is of great interest to identify possible underlying variables. We measured novelty response, inhibition and aspects of exploratory behaviour. Because Sumatrans were more cautious in tasting novel food (Figure 5), better performance was not due to reduced neophobia, as was found in some previous studies (Benson-Amram & Holekamp, 2012; Cauchard *et al*., 2013; Sol *et al*., 2012). The species difference was also not confounded by age effects. Although younger Sumatrans delayed their intake of novel food, when tested individually (Figure 5B), the species difference remained even when we excluded the younger subjects from the Sumatran sample. Species with greater dependence on social learning have been suggested to also exhibit higher neophobia and conservative novelty response, because they strongly rely on social cues to engage in independent exploration (Forss *et al*., in prep). However, captivity has been shown to suppress neophobia in orang-utans (Forss *et al*., 2015). Therefore, it is remarkable that we still detect this species difference in a zoo comparison, suggesting a stronger predisposition for cautiousness in Sumatran orang-utans than Borneans.

In the honey tool-task, which consisted of multiple problem-solving steps, both species were equally keen on participating and spent equal time exploring the task (Figure 7A), but Sumatran females, though not males, spent more time exploring the relevant parts of the apparatus (the holes containing honey; Figure 8). Further, Bornean orang-utans were more likely to apply a rougher exploration style than their Sumatran relatives, both in the detour-reaching box and toward the novel toy (Figure 6B and 6D). Such rough actions suggest that the subjects had given up on trying to find a solution and were either frustrated or attempting to reach the food reward through force, or both.

Reversal-learning tasks entail an element of inhibition (Bond *et al*., 2007; Griffin *et al*., 2015). A higher percentage of Sumatran individuals learned the colour reversal. Although this was not significant, we found that Sumatrans were also better at inhibiting their behaviour in that they opened significantly fewer lids of the wrong colour than Borneans (Figure 9). Orang-utans have previously been reported to exhibit higher inhibitory control than other great apes (Manrique *et al*., 2013), but our results suggest that Sumatrans show this even more than the Borneans, which complements their greater cautiousness and gentler explorative behaviour.

In sum, the superior cognitive performance by the Sumatran orang-utans may well reflect their greater inhibitory control and more cautious exploration style, which made them less likely to turn to destructive exploration and more likely to focus on relevant aspects of the problem at hand.

Because group size in the zoos examined did not affect the results and the zoos did not differ greatly in their enrichment regimes, this species difference cannot reflect any differences in opportunities for social or asocial learning during development other than those caused by innate differences in

attention patterns or social tolerance by role models. Moreover, it is unlikely to be due to innate differences in the ability to effectively manipulate tools, because on Sumatra the tendency to use tools is limited to particular regions (van Schaik *et al*., 2009). Zoo orang-utans of both species use tools regularly and all nine zoos where the data was collected provided the apes with enrichment devices requiring stick tool-use, with which all subjects in our study were familiar.

If the species had been very different in overall or relative brain size, the same result would presumably have been obtained, given the effect of brain size on cognitive abilities in primates (Deaner *et al*., 2007; Reader & Laland, 2002) and carnivores (Benson-Amram *et al*., 2016). The study was designed to capture the effects of cultural intelligence at similar brain size. Nonetheless, there are minor brain size differences between the two orang-utan species. Although females are all approximately the same body size, those of the two western Bornean subspecies have a cranial capacity that is slightly (average 2-3%) smaller than that of the Sumatrans. However, those of the eastern subspecies *Pongo pygmaeus morio* have a cranial capacity that is on average 11-12% smaller than that of the other Bornean subspecies and 14% smaller than that of the Sumatrans (Taylor & van Schaik, 2007). However, because the breeding program in European Zoos that manages the population of *Pongo pygmaeus*, does not distinguish between subspecies, we do not know which individuals, if any, are of this subspecies, assuming there are any pure or hybrid *P. p. morio* at all in European zoos. Moreover, the brain size distributions between the species and subspecies show high overlap, and any difference in relative brain size is still less than that between the sexes of modern humans (Ankney, 1992; Lüders *et al*., 2002; Lüders *et al*., 2009). Furthermore, in many tests of cognitive abilities, the various great apes do not differ consistently in their cognitive performance (Amici *et al*., 2012; Call, 2006; Hanus & Call, 2007; Vlamings *et al*., 2006; Vlamings *et al*., 2010), despite greater interspecific differences in absolute and relative brain size than found between Bornean and Sumatran orangutans. Most importantly, however, regardless of any residual effects of brain size, we identified plausible underlying causal differences in exploration style, which help us understand the species differences found here and may also be involved in species differences across a broader range of brain sizes (e.g. inhibitory control, see MacLean *et al*., 2014).

4.6 Conclusion

This species comparison of physical cognitive tasks provides the first empirical confirmation of the cultural intelligence hypothesis in a non-human species, suggesting that the combination of more frequent opportunities for social learning and advanced skill repertoires have over evolutionary time produced cognitive differences between the two *Pongo* species. We saw that they differ in physical problem-solving performance but also in some of the likely underlying mechanisms, including

inhibitory control and caution, traits that may very well be the ones targeted by selection on learning abilities, and thus crucial for effective cultural learning.

4. 7 Acknowledgements

We thank all the following zoological gardens for their collaborations and contribution to our study: Zoo Dortmund, Twycross Zoo, Durrell Wildlife Trust, Allwetterzoo Münster, Zoo Basel, Apenheul Primate Park, Wolfgang Köhler Primate Center at Leipzig Zoo, Blackpool Zoo and Paignton Zoo. Special thanks to all the zoo keepers who helped with the experimental set ups. We are grateful to Daniel Haun, Katja Liebal and Judith Burkart for their feedback and inputs while developing the set of experimental task. We also express our gratitude to the following foundations who have financially supported this project: A. H. Schultz Foundation, Paul Schiller Foundation and the Claraz Foundation in Switzerland and Waldemar von Frenckells Foundation, Ella and Georgh Ehrnrooths Foundation, Otto A. Malms Donationsfond, Nordenskiöld Samfundet and Oskar Öflunds Foundation in Finland.

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Chapter 5

Human Induced Curiosity Predicts Cognitive Performance in Orangutans

Published in Scientific Reports January 2017

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5.1 Abstract

Non-human animals may show great intraspecific variation in their cognitive abilities. Especially in large-brained species external inputs and experiences during the prolonged developmental time is expected to modify cognitive mechanisms. We examined the variation in exploration and cognitive performance on a problem-solving task in a large sample of captive housed orangutans (*Pongo abelii* & *Pongo pygmaeus*, N=103) in relation to variation in conditions during ontogeny, including in duration of exposure to humans. In addition to measuring cognitive performance we also conducted a set of experiments to assess the subjects' psychological attitude, including reactions toward a novel human and novel food or objects. Based upon the response to an unfamiliar human we created a human orientation index (HOI) in order to quantify variation in attentiveness of individuals with different rearing histories. Using general linear mixed models we found human orientation, but not neophobia, to predict both exploration variety and problem-solving skill. We conclude that different experiences with humans made individuals vary in curiosity and understanding of physical problem-solving tasks. We discuss the implications of these findings for comparative studies of cognitive ability.

5.2 Introduction

As in humans, individual performance on a variety of tests of cognitive ability, including problem-solving tasks, is correlated in various non-human primate species, leading to suggestions that they too show evidence of general intelligence (Herndon *et al*., 1997; Reader & Laland, 2002; Banerjee *et al*., 2009; Reader *et al*., 2011; van Schaik & Burkart, 2011; Woodley de Menie *et al*., 2015). Human intelligence is partly genetically determined and thus inherited (Burt, 1972; Plomin & Petrill, 1997 ; Davies *et al*., 2011 ; Nisbett *et al*., 2012 ; Bates *et al*., 2013 ; Turkheimer *et al*., 2013; Joshi *et al*., 2015). This finding was recently confirmed for our closest living relatives, the chimpanzees (Hopkins *et al*., 2014). As expected based on the great developmental plasticity of especially cortical brain functions (Quartz & Sejnowski, 1997), human intelligence is also strongly affected by the conditions experienced by the developing individuals, from early nursing experience (Anderson et al., 1999; Mortensen *et al*., 2002; Der *et al*., 2006; Kramer *et al*., 2008) to cultural impacts later in life (Bouchard *et al*., 1990; Markus *et al*., 1991; Neisser *et al*., 1996). Much less is known about this phenomenon in nonhuman primates, where variability is often regarded as "noise" in species comparisons.

Our knowledge of intraspecific variation in cognitive abilities among primates so far has mainly come from two extreme cases of experience effects: *deprivation* and *enculturation*. Harlow's pioneering experiments on rhesus macaques demonstrated strong negative outcomes of physical- and social-deprivation on cognitive development (Harlow & Zimmerman, 1959; Gluck & Harlow, 1971; Gluck *et al*., 1973). Since then other primate studies have pointed out maternal separation to have both short-

and long term socio-cognitive consequences (Gilmer & McKinney, 2003; Freeman & Ross, 2014; Kalcher-Sommersguter *et al*., 2015). Skills linked to physical cognition also tend to be influenced by early rearing conditions. Chimpanzees that were removed from their mothers as young infants showed reduced competence in both nest-building (Videan, 2006) and problem-solving skills involving tool use (Menzel *et al*., 1970; Morimura & Mori, 2010). Although deprivation affects the expression of primate intelligence, it could be argued that these extreme conditions remove inputs for experience-expectant processes (Greenough *et al*., 1987), and thus reflect different processes from the ones affecting cognitive variation in humans.

The opposite extreme condition is enculturation. Especially among great apes (but see Fredman & Whiten, 2008), enriched socio-cultural inputs, in the form of extensive training by humans, result in enhanced cognitive skills, particularly in socio-cognitive and communicative abilities (Tomasello *et al*., 1993; Call & Tomasello, 1996; Tomasello & Call, 2004; Rumbaugh & Washburn, 2003; Bering, 2004; Björklund, 2006). Enculturated apes also show faster development of motor skills, sophisticated object manipulation and more skillful tool use (Bard & Gardner, 1996; Gardner & Gardner, 1989; Furlong *et al*., 2008). It remains possible, however, that social inputs far beyond the range found under natural conditions may reflect the operation of processes not normally present during development.

Even in the absence of deprivation and enculturation, captive primates may show high intraspecific variability in cognitive abilities (Herrmann *et al*., 2010; Herrmann & Call, 2012). Similarly, recent work has found high variability in problem-solving abilities of wild mammals (e.g. Liker & Bókony, 2009; Cole *et al*., 2011; Benson-Amram & Holekamp, 2012; Thornthon & Samson, 2012; Cauchard *et al*., 2013; Griffin & Guez, 2014). However, the strongest intraspecific variation in cognitive traits is found between wild and captive individuals of the same species (e.g. Visalberghi *et al*., 2003; Laidre, 2008; Benson-Amram *et al*., 2013; Forss *et al*., 2015).

The sources of this variability remain largely unstudied. There is therefore a need for comprehensive studies of individual variation in cognitive performance that can be related to the individuals' rearing histories and the underlying psychological motivational and emotional variables, such as motivation to solve problems, responses to novelty and exploration style. Such studies are best conducted in captivity, where experiments can be made more uniform, individual histories usually are better documented, and the underlying psychological variables can be estimated independently.

These differences in cognitive performance may have various causes. Captivity changes how animals respond to novelty, expressed by strongly reduced neophobia compared to wild conspecifics (Visalberghi *et al*., 2003; Benson-Amram *et al*., 2013; Forss *et al*., 2015; Forss *et al*., in prep). The contrast in novelty reactions can to a certain extent explain variation in cognitive performance when assessed experimentally: due to reduced neophobia captive hyenas outperformed their wild

conspecifics when tested on their problem-solving abilities (Benson-Amram *et al*., 2013). However, the effect of captivity is not restricted to novelty response, because the absence of neophobia may trigger further cognitive changes. Extractive foragers, such as primates increase explorative behaviors, tool use and innovation rates in captivity (Russon, 2003; Lehner *et al*., 2010; Shumaker *et al*., 2011; Haslam, 2013; van Schaik *et al*., 2016). This increase in creative behavior especially among captive primates has so far been attributed to reduced costs associated with ecological causes such as time constraints, predation risk and terrestriality (Kummer & Goodall, 1985; Meulman *et al*., 2012; Benson-Amram *et al*., 2013; Haslam, 2013; van Schaik *et al*., 2016), whereas social influences have received less attention. This is remarkable given that captive environments expose primates with a strong social component of human exposure. In their natural niche primates are prone to attend to conspecifics and learn necessary skills socially (Lonsdorf *et al*., 2006; Humle *et al*., 2009; Jaeggi *et al*., 2010; van de Waal *et al*., 2010; van de Waal *et al*., 2013; Schuppli *et al*., in prep). Consequently having evolved to be attentive to others' activities, captive primates experience increased social opportunities that besides conspecifics include human role models. Accordingly from birth on the attention structure of captive primates may be tuned toward human cues, upon which further cognitive differences may follow.

In the present study, we ask how a range of different captive management regimes affects both independent psychological attitudes, such as human orientation, motivation and exploration style, and cognitive performance in more than 100 captive orangutans, *Pongo abelii* and *P. pygmaeus.* In both wild and captivity, orangutans are known to be flexible problem solvers, as suggested by their large innovation repertoires (van Schaik *et al*., 2006) and their strong scores on comparative cognitive tests (Deaner *et al*., 2006; Reader & Laland, 2002). It is widely assumed that this ability is adaptive in their challenging foraging niche, for which developing individuals must learn the requisite skills over several years (Jaeggi *et al*., 2010; Schuppli *et al*., 2016).

Our sample contains both zoo groups of orangutans, consisting of both mother- and hand-reared individuals, and individuals housed in rehabilitation stations from a diverse range of backgrounds: station-born animals and orphans who are wild-born and experienced variable duration in the wild and subsequent captivity, as well as former pets. The availability of individuals kept under highly similar conditions but with a wide range of rearing histories provides us with an excellent opportunity to test their effect on cognitive performance and exploration styles. Because the individuals' experience with humans was so variable, we conducted the study without the presence of an experimenter to avoid possible effects on the subject's participation and attention during cognitive testing (cf. Schubiger *et al*., 2015).

First, we examined the subjects' performance on a novel, multi-step problem-solving task with high ecological validity: the honey-tool task. Second, we assayed the individuals' psychological attitudes underlying their exploration style. Because the captivity effect on cognitive performance seems to

reflect the most dramatic change in psychological attitude, we developed the human orientation index (henceforth: HOI) as a predictor of cognitive performance and exploration style (see Methods for details). Moreover, as orangutans show increased interest in novelty in captivity (Forss *et al*., 2015), we also assessed the response to novelty across individuals of different captive conditions. Third, we broke down our sample according to housing conditions. Zoos and rehabilitation stations differ in their purpose of holding captive apes. Zoo apes have lived all their lives in a similar and stable environment, mostly together with their mothers and in intense contact with both knowledgeable conspecifics and human caretakers, with additional exposure to human strangers on a daily basis. Virtually all zoos also offer enrichment in the form of various foraging activities. In rehabilitation stations the purpose is very different. Many individuals have experienced traumatic events in their past (capture and loss of mother, sometimes accompanied by injury) and thus need to recover physically and mentally. The stations' ultimate aim is to bring individuals back into the wild, and consequently they avoid bringing about too close an attachment to humans or exposing them to artificial enrichment devices. Moreover, many rehabilitating apes lack the close bond to their mother or other knowledgeable adults and are instead housed in peer groups.

Our overall aim, then, is to relate the variation in rearing histories to psychological attitudes and exploration styles, and thus to problem-solving abilities. The results of this study should also help to improve comparability when the cognitive performance of different species is compared.

5.3 Methods

5.3.1 Subjects and study locations

Our total sample size involved 103 orangutans: 68 *Pongo pygmaeus spp* and 35 *Pongo abelii*. Data collection on the zoo-housed sample took place at nine different European zoos between November 2012 and January 2015 and all data was collected by SF (Table 1). In total the zoo sample consisted of 41 individuals, of which 31 were standard mother-reared and ten individuals whose own mother had either died or rejected the infant were hand-reared: cared for by human caretakers, within the zoo or partly within a human household, and subsequently returned to a group of zoo-living conspecifics (Table 2).

Data on 62 rehabilitation orangutans was collected between June 2012 and June 2014 by LD and ZK, supported by a trained assistant Andreas Wendl. In Borneo data was conducted at the Orangutan Care Center and Quarantine (OCCQ) and Nyaru Menteng Rescue Center managed by Bornean Orangutan Foundation International (BOSF), both located in Central Kalimantan (Table 1). In Sumatra data collection took place at two sites managed by the Sumatran Orangutan Conservation Program (SOCP):

the quarantine station in Batu M'Belin (QBM) and at the release site Danau Alo, Bukit Tigapuluh in Jambi (Table 1).

Depending on available background information the sample collected at the rehabilitation stations was further divided into following defined groups: Wild, Station, Ex-Human and Unknown. Individuals were assigned to these four groups depending on at what age they had arrived at a rehabilitation station and their previous history with humans (Table 2).

Table 1: Overview of subjects and study facilitations.

Study Facility	N	Species	Age Range	Social Housing	Test Location	Time Period
Münster zoo	6	*P. pygmaeus*	6-43	Mixed-age group	Sleeping box	Apr-May 2013
Apenheul primate park	8	*P. pygmaeus*	13-52	Mixed-age group	Sleeping box	Jan-Feb 2014
Basel zoo	4	*P. abelii*	5-13	Mixed-age group	Smaller enclosure	Nov 2013
Blackpool zoo	4	*P. pygmaeus*	13-31	Mixed-age group	Sleeping box	Jan 2015
Dortmund zoo	4	*P. abelii*	8-23	Mixed-age group	Sleeping box	Nov-Dec 2012
Durrell wildlife trust	5	*P. abelii*	9-49	Mixed-age group	Sleeping box	Mar 2013
Leipzig zoo	6	*P. abelii*	5-25	Mixed-age group	Test enclosure	Mar 2014
Paignton zoo	2	*P. pygmaeus*	18-20	Mixed-age group	Sleeping box	Feb 2015
Twycross zoo	2	*P. pygmaeus*	14-36	Mixed-age group	Sleeping box	Jan-Feb 2013
Danau alo/ SOCP	5	*P. abelii*	3-6	Solitary	Home enclosure	Apr-Jun 2013
Nyaru menteng	18	*P. pygmaeus*	6-17	Solitary	Home enclosure	May-Jun 2014
OCCQ	28	*P. pygmaeus*	8-14.5	Peer group	Test enclosure	June-Sep 2012
Batu mbelin/ SOCP	11	*P. abelii*	5-25	Solitary	Home enclosure	Oct 2012-Mar 2013

5.3.2 Housing conditions

In the zoos, individuals were housed in mixed-aged groups of conspecifics ranging from four to 12 individuals in standard indoor enclosures during the day, and mostly separated individually or in pairs into sleeping boxes for the night. Most zoos also provide the orangutans with a larger outdoor enclosure. At each zoo, animal keepers are in daily close contact with the orangutans, providing them with food but also with diverse enrichment activities.

In the rehabilitation stations the housing situations were more heterogeneous (see Table 1). They differed according to the standards and capabilities of each facility and the age, sex and background of the individuals. All orangutans in this study were at the time of the study held in solitary cages, except for one station were 28 individuals were socially housed in groups of 2-6 individuals. Contact with humans was limited: caretakers were cleaning and feeding several times a day, and if necessary veterinarians took care of their physical health. Each cage had simple enrichment devices, such as ropes, and once a day subjects received extra food-related enrichment. If the infants were very small human caretakers served as a mother replacement. These individuals were attended to in a nursery

home with other infants. They had daily contact and supervision by humans for their needs. Most individuals had access to the forest at some stage during their time at the station.

Table 2: Groups of subjects and their background information.

Group	N	Age Range	Current Housing	Years in Captivity	Human Exposure	Remark
Wild	5	10-25	Rehabilitation station	0-7	Minimal	Majority of life in natural habitat. Arrived at a rehabilitation center as sub-adults or adults, eventually to be translocated to a new natural habitat.
Station	8	5-11	Rehabilitation station	4-10	Mainly human raised.	Minimum 80% of life in rehabilitation station. Arrived at station as dependent offspring at the age of 1.5 year or younger.
Ex-Human	16	3.5-14	Rehabilitation station	0-9	Minimum 6 months with humans	Arrived at rehabilitation station after the age of 1.5 years. Background history with human contact i.e. pet (minimum 6 months)
Unknown	33	3-17	Rehabilitation station	0.5-14	Unknown before arrival at station	No background information. Arrived at station between 2 and 7 years of age and therefore large part of the developmental phase spent in captivity.
Mother-reared Zoo	31	5-52	Zoo	Whole life	All life within human care	Nursed by own mother within a zoo. All life in captivity with exposure to human caretakers and visitors.
Hand-reared Zoo	10	13-43	Zoo	Whole life	Human hand nursing and all life within human care	Nursed by human caretakers either at the zoo or in human households. All life in captivity with exposure to human caretakers and visitors.

5.3.3 Human Orientation Index

To capture any psychological variation caused by time in captivity and human-related experiences, we assessed the degree to which each individual reacted toward a novel human. The Human Orientation Index (HOI) contained the following components: reactions and proximity to a human stranger during two conditions. Each subject was tested individually, except for a few cases where the mother was tested with its dependent offspring to avoid inducing stress for both. In the zoos the test took place either in the home enclosure or in the sleeping quarters if individuals were more easily separated there. In the rehabilitation stations, individuals were either transported to single compartments for testing or were directly tested in their home enclosure. The test was performed by a local man, unknown to the orangutans and dressed in black.

The total test lasted for one minute and was composed of two consecutive conditions, each lasting 30 seconds. In the first condition the man approached and positioned himself approximately one meter in front of the enclosure where the subject was located and remained standing with his body oriented laterally (perpendicularly) to the subject. In the second condition the man turned around to face the orangutan and tried to establish eye contact. The whole test was video recorded and during the entire test no other human was present.

Reactions and proximity to the man for the first two seconds of first sight were coded from the videos. For each condition we scored the proximity to the man in the following way: 0= the orangutan positioned itself as far away as possible; 1= the orangutan was more than one meter away from the human; 2= the orangutan was within one meter from the human; and 3= the orangutan placed itself as close to the human as possible.

We also scored the very first behavioral reaction of the orangutan for each condition as follows: 0= a negative reaction, defined as: retreat, stress vocalization, pilo-erection, nervous swinging or turning away from the human; 1= a neutral reaction, defined as resting, moving calmly or play behavior; 2= a positive reaction, if the orangutan approached the human; and 3= an actively positive reaction, if the orangutan begged (either by using lips or hands), tried in any other active way to contact the human or attempted to trade objects from the enclosure for food.

Furthermore, since the measurements listed above were based upon the first reaction of each condition only, we also scored whether any active contact behavior occurred during the 30 seconds of each condition. This was to ensure catching the possible substantial interest in humans, when the surprise had waned.

Thus, in total HOI consisted of all the summed behavioral reactions combined with the proximity to a human stranger, with the eventual score ranging from zero to 14. In our sample, scores ranged from 2 to 14. Furthermore, we also measured the time in seconds a subject spent within one meter of the human stranger throughout the whole test and found that this independent time measurement of proximity was strongly correlated with the HOI-index (Spearman's correlation, two-tailed: $r^s=0.600$, N=96, P<0.001). Given that an individual can be in close proximity and not move throughout the time of the test, but nevertheless not show any active response behavior, we used the summarized index of both behavioral reactions and proximity scores, which also generated more resolution to the various responses within our sample, than simply proximity latency data would.

The logistics in one of the rehabilitation stations allowed us to use a sub-sample of 28 individuals to test for social interest in unfamiliar conspecifics. In this sub-sample we measured the time of close proximity to two other unknown orangutans of equal sex, when these were present in a neighboring enclosure to the subject, which allowed us to disentangle social orientation per se to that from interest in humans.

5.3.4 Response to novelty

We performed two separate tests to assess individual variation in novelty response. First, we examined how each subject reacted to novel food. In the zoo sample the novel food was blue potato mash served with black olives on top. Zoo orangutans receive a broad diet with many types of human food, but blue items are not common and olives were new to all individuals. In the rehabilitation stations we used purple rice or purple potato mash. Second, we introduced a novel toy in form of a wooden board equipped with six different colored rotatable tennis balls. For both tasks, we recorded the latency to first touch or first taste, respectively, as well as exploration duration of the novel toy. Maximum test duration was two minutes for both tasks, and each subject was tested individually.

5.3.5 Experimental cognitive task – The honey tool-task

In order to evaluate cognitive performance we used a naturalistic task, which required no pre-training trials and could therefore easily be applied to all individuals. The honey tool-task allowed us to assess physical cognition at multiple levels from very basic understanding of the apparatus to high innovativeness. The task was made up of a wooden box measured 50 cm x 80 cm x 5 cm, whose front was covered by a transparent plexiglas plate (Figure 1). The upper part of the box contained a straight channel (30 cm x 5 cm) in which sat a pre-inserted wooden stick (40 cm) with its tip dipped in honey. Below the straight channel, the box also had another channel, which was L-shaped. This channel was 15 cm x 10 cm and the bottom of the curve was filled with honey. The honey was visible to the subjects through the plexiglas but the length of the channel was too long for any finger to reach the honey. Moreover, the wooden stick would not work in the L-shaped channel. In addition, below the test apparatus we provided each subject with two more wooden sticks and three pieces of rope. The ropes were too short to reach the end of the straight channel but long enough to bend the L-shaped curve and retrieve honey from its bottom.

We measured multiple aspects of the subjects' responses to the apparatus, which was presented to them in the absence of any humans. To estimate cognitive ability, we measured the following actions: 1) removing the provided stick from the straight channel; 2) inserting any of the three provided sticks into the straight channel during total test time; 3) tool manufacturing, defined as an attempt to modify the provided tools and/ or the use of any other tool that the subject found or made; 4) inserting the rope tool into the L-shaped channel. We recorded each task measurement individually with yes or no, depending on whether or not a subject completed the action (Table 3).

We also recorded detailed data on any exploration actions during the problem-solving task. These were divided into two main categories: relevant and irrelevant exploration. Relevant exploration involved any exploration of the channels, and thus the actual problem to be solved. Any other explorative acts directed toward the test apparatus itself, the board or table on which it was presented was counted as irrelevant exploration. For our statistical analyses, we measured the frequency and variety as well as duration of both categories of exploration.

A **B** **C**

Figure 1: A zoo housed subject exploring the honey tool-task (**A**). The honey tool-task in the zoos (**B**) and rescue centers (**C**).

Table 3: Measurements of cognitive performance

Task measurement	Definition	Remarks
Remove stick	Stick provided in the straight trap is taken out of the trap	Recognition of the stick in the trap and removal of it
Insert stick straight trap	Any of the three sticks are inserted into the straight trap during the 10 minutes test time	Understanding of stick fitting the straight trap
Tool manufacture/ other tool use	Any tool (stick or rope) is modified or any other material is used as a tool in any of the two traps	Innovative attempt to retrieve honey by modifying existing tool or trying out any other solution
Insert rope to L-shaped trap	Any of the three ropes are inserted into the L-shaped trap	Understanding of the properties of rope fitting the L-shape trap

5.3.6 Experimental procedure

A In all tasks; novelty response tests, the HOI test and the honey tool-task only those individuals who were easily and voluntarily separated for the experiment participated, therefore sample size between the different tests varied between 94-103. In the honey tool-task each orangutan was tested individually, except for mothers who could not be separated from their dependent offspring, in which case the offspring was not participating in the task. All subjects were naïve to this test apparatus and we performed no training trials. Thus each subject was tested only once. Zoo individuals were tested in their smaller sleeping enclosures where they could be separated from the group. In the

rehabilitation stations testing took place in their home cage, since most individuals were housed alone. For the 28 socially housed individuals, additional testing cages were available. The individuals were brought to the testing cages separately and only stayed there for the time of testing. The problem-solving task lasted for a maximum of 10 minutes and no humans were near the subjects during this time. The task was video recorded with one to two SONY HDR-CX200 handy cameras, depending on angle of the cameras. All subjects were normally fed both before and after testing and thus were not food-deprived for the task. In the rehabilitation stations, the honey tool-task was presented to the subjects on a large board right outside of their enclosure, and subjects could easily reach out toward the problem-solving task. In one zoo, we were able to present the honey box within the test enclosure and thus subjects here had full access to the apparatus. In all other zoos the logistics were slightly different and due to narrower mesh size the apparatus was therefore presented closer to the mesh outside the enclosure, with a slight angle but less accessible to the subjects. We therefore scored accessibility of the test apparatus and controlled for this variation in the statistical model.

5.3.7 Data extraction and statistical analyses

All videos were imported into Mangold interact 9.7, where all detailed behaviors of both cognitive performance measurements as well as exploration acts were coded by SF and LD. We used IBM SPSS statistics 20 to perform inter-observer reliability tests on every detailed behavioral act. For the zoo sample, 20% of the videos were coded by both observers and yielded a Cohen's Kappa value of 0.842 (N_{events}=1020, P=0.000), which is considered very good. From the rehabilitation sample, 16% of the videos were coded by both observers and delivered a good inter-rater agreement (Cohen's Kappa: 0.721, N_{events}=1020, P=0.000). All statistical analyses were performed in R version 3.2.3 (Team R Core: 2015) using a binomial General Linear Mixed Model (GLMM) to examine each individuals performance as well as Linear-Mixed-Effect-Models (LMM) for assessments of the relationship between the HOI-index, novelty response, exploration variables and performance.

5.3.8 Ethical note

All experiments fully complied with the ethical guidelines of each study facility and were respectively approved by the research manager and/or head of each facility. We confirm that according to the Swiss Animal Welfare legislation our animal experiments are considered with the severity grade 0 (no harm). The experimental protocols for the rehabilitation stations were approved by the Animal Welfare office of the University of Zurich, the Scientific Advisory Board of the BOS Foundation (Bornean Orangutan Survival), the research managers and head of the stations of Sumatran Orangutan Conservation Programme (SOCP) and Orangutan Foundation International (OFI), and the Indonesian Ministry of Research and Technology (RISTEK). Moreover, all zoo experiments were supported by research committee of the British and Irish association for zoos and aquariums, BIAZA.

5.4 Results

5.4.1 Cognitive performance

For the honey tool-task, we found large variation in cognitive performance among the 103 orangutans (Figure 2). Eleven individuals did not solve a single sub-task. The modal and median score on total performance was 1 out of a maximum of 4. The four different cognitive measurements of the honey tool-task varied significantly in difficulty. In order to examine whether the ability to solve the different sub-tasks was cumulative, we applied a Guttman scale, which showed a reproducibility coefficient of close to one (0.97). This strongly suggests that the ability to solve the more difficult sub-tasks was nested within the performance of the other sub-tasks: 90% of the 103 individuals performing the honey tool-task fitted the applied Guttman scale of the four different sub-tasks. As expected, 'remove stick' was the easiest, 'insert the stick in the straight channel' was next, followed by 'making a tool', whereas 'inserting the rope in the curved channel' was most difficult (Table 3, Sub-task) for the orangutans in this study. Due to this variation in difficulty, we treated the four levels of cognitive performance as an ordinal variable in further analyses.

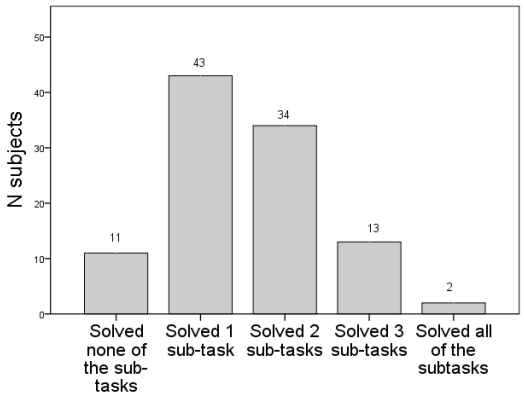

Figure 2: Honey tool-task performance. Frequency of subjects that solved zero to all subtasks.

We next tested whether background and housing conditions, species, sex, and age could explain the variation in cognitive performance on the honey tool-task. Table 1 shows the results of a binomial Generalized Linear Mixed Model (GLMM) of the honey tool-task performance, with the response variable being whether or not a subject solved each sub-task. The GLMM allowed us to control for repeated observations in each facility and on each individual. The results revealed that the human orientation index (HOI) was a good predictor of the ability to solve the task (B±SD= 0.227±0.08, Z=2.699, P=0.007; Table 4), as was the latency to touch unfamiliar food (B±SD= -0.034±0.01, Z=-2.263, P=0.024; Table 4) and a novel object (B±SD= -0.025±0.01, Z=-2.123, P=0.034; Table 4). The less neophobic the individuals, the more likely they were to solve the task. When we removed the novelty responses from the analysis, the HOI remained the main predictor of performance (Table 5, Appendix III). Because an individual's age and the time it had spent in captivity were strongly correlated, only the factor age was considered for the analysis, but it did not influence task performance. Subtle differences between enclosures, which might affect the ease of access to the apparatus, were controlled

for in the analysis, but again did not contribute to explaining the variation in cognitive performance. Perhaps surprisingly, none of the other possible variables (sex, species [Sumatran or Bornean], and the various background and current housing conditions of the orangutans) predicted performance; they also had no influence on task performance when HOI was excluded from the analyses (Table 6, Appendix III).

Table 4: Generalized Linear Mixed Model of overall performance in the honey tool-task.
Parameter estimates from a binomial GLMM, predicting the probability of an animal solving the task.

	B	*SE*	*Z*	*p value*
(Intercept)	-2.588	1.33	-1.943	0.052
Human Orientation Index	0.227	0.08	2.699	**0.007 ****
Novel food: time until touch	-0.034	0.01	-2.263	**0.024 ***
Novel object: time until touch	-0.025	0.01	-2.123	**0.034***
Novel object: exploration duration	0.003	0.01	0.433	0.665
Age	-0.006	0.03	-0.232	0.817
SEX (male)	0.124	0.51	0.243	0.808
Species (Sumatra)	-0.094	0.59	-0.16	0.873
Background				
Wild vs. Rest	-0.173	0.27	-0.639	0.523
Rehab vs. Zoo	-0.402	0.29	-1.395	0.163
Unknown vs. Rehab.Rest	0.073	0.20	0.367	0.714
Human vs. Station (within rehabilitation station)	-0.479	0.48	-1.008	0.314
Mother vs. Hand (within zoo)	0.365	0.51	0.722	0.470
Accessibility (trend analysis)				
Linear	0.786	0.76	1.04	0.298
Quadratic	0.228	0.89	0.257	0.797
Cubic	-0.189	0.89	-0.213	0.831
Sub-task (trend analysis)				
Linear	-4.969	0.74	-6.737	**<0.001 *****
Quadratic	1.554	0.44	3.559	**<0.001 *****
Cubic	-0.205	0.33	-0.626	0.531

Note: The model is controlling for repeated observations on each facility and individual. The performance in the honey tool-task was binary measured. The Analysis included 88 individuals in 9 different zoos/rehab stations, totalling 352 observations, χ^2= 226.27, *P*< 0.001, P-values below 0.05 appear in bold.

5.4.2 Exploration behavior

The orang-utans' performance on the tool-use task was best accounted for by exploration variety, which explained 27% of the variation (Figure 3 and Figure 4b), whereas exploration duration predicted 9% of the variation (N_{obs}=94, $N_{location}$=10, χ^2_{ML} =08.57, $R^2_{LMM(m)}$=.092, P =0.005, Figure 3 and Fig. 4a). However, the HOI only explained 5% of cognitive performance (χ^2_{ML} =6.21, P<0.05).

The effect of human orientation on exploration

A Linear Mixed-Effects Model (LMM) analysis of the subjects' exploration of the apparatus, which controlled for repeated measurements in each facility, showed that HOI accounted for 11% of the variation of the total exploration variety (N_{obs}=94, $N_{location}$=10, χ^2_{ML} =12.02, $R^2_{LMM(m)}$=0.1113, P <0.001, Figure 3 and Figure 5b). In addition, there was a trend showing that individuals with a higher HOI explored the apparatus longer than those with a lower HOI (N_{obs}=94, $N_{location}$=10, χ^2_{ML} =3.53, $R^2_{LMM(m)}$=0.025, P =0.06, Figure 5a), although the HOI explained a mere 2% of the variation in exploration duration (Figure 3). This low proportion is not surprising, because the most successful orang-utans, and thus the ones with high HOI values, stopped exploring once they found the solution to the problem and spent their remaining time extracting honey.

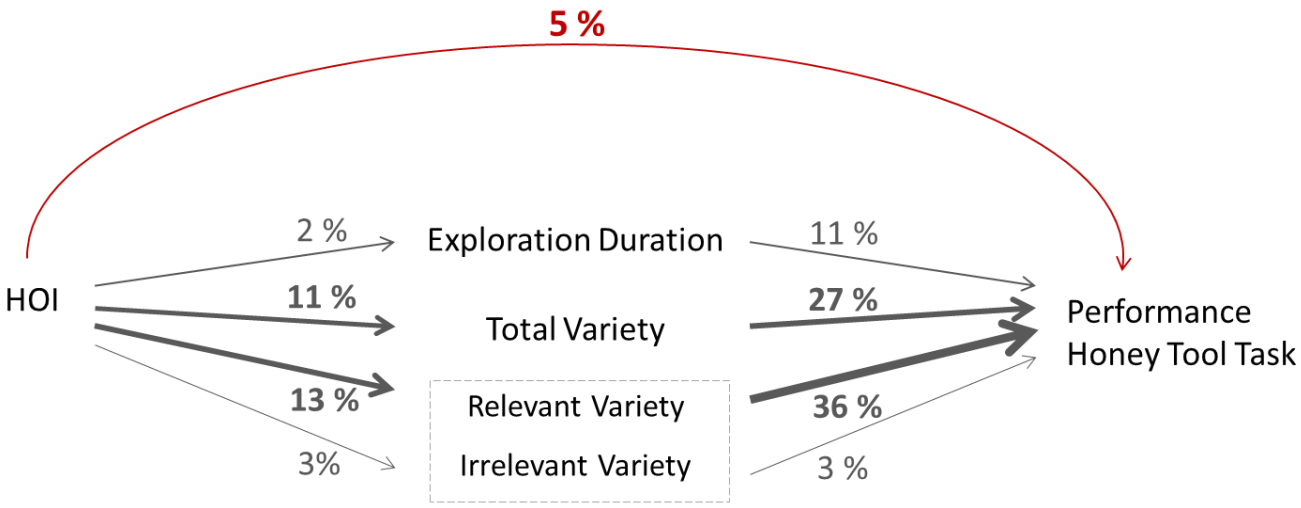

Figure 3. Graphical illustration of the relationship between the human orientation Index (HOI), the cognitive performance and exploration duration and variety, in context to each other. The total variety can be divided into relevant and irrelevant variety. The figure also indicates the percentage of variation estimated by the pseudo R2 for linear mixed effects margins that is explained by each factor. The thickness of the arrows accentuates the strength of the influence.

Random exploration of the apparatus per se does not necessarily raise the chances of finding the solution. Individuals who can distinguish between relevant and irrelevant parts of the apparatus should be more successful (Table 7, Appendix III). We therefore also investigated the separate effects of exploration variety directed at the relevant or irrelevant areas of the apparatus. We calculated marginal pseudo-R^2 values to estimate the proportion of variation explained by the fixed effects in our model. The HOI explained 13% of the variation of relevant exploration (χ^2_{ML} =13.67, P<0.001, Figure 3 and Table 8, Appendix III), which subsequently accounted for 36% of the variation in cognitive performance. In contrast, HOI explained only 3% of the irrelevant exploration (χ^2_{ML} =2.93, P=0.087, Figure 3), which accounted for only 3% of performance in the task. The effect of a higher HOI was thus primarily on the amount of exploration and especially on the diversity of exploration on relevant parts of the task, with the latter explaining 36% of cognitive performance. Furthermore, neither housing- nor background/ rearing history had any effect on the exploration of the apparatus (Table 8, Appendix III).

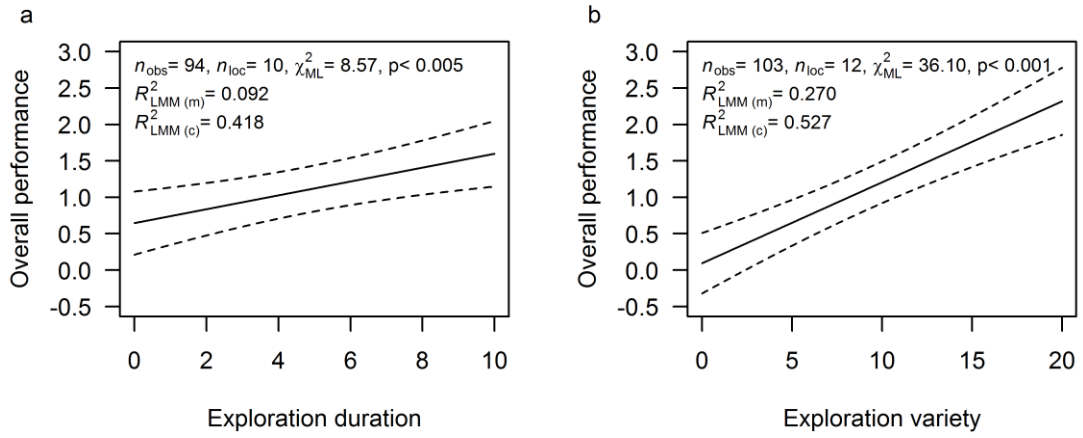

Figure 4. The relationships between exploration behaviour and the overall cognitive performance. (**a**) Overall performance in relation to the exploration duration. Individuals that explored longer were significantly better problem solvers (N_{obs}=94, $N_{location}$=10, χ^2_{ML} =08.57, P =0.005). (**b**) The overall task performance in relation to the total variety of exploration actions (N_{obs}=103, $N_{location}$=12, χ^2_{ML} =36.10, P <0.001).

Additionally, using a Linear Mixed-Effect Model (LMM), controlling for each subject's housing location, we compared the exploration style of the most successful individuals, the 10 subjects who solved the most difficult problem of 'inserting the rope in the curved channel' ('ropers'), to the other non-successful individuals ('non-ropers') (Figure 6). There was no difference in exploration duration between ropers and non-ropers. However, the ropers differed significantly from non-ropers in their exploration variety (P= 0.012). Ropers not only showed a greater diversity of explorative actions, but also a far greater diversity of exploration on relevant parts of the apparatus (p< 0.001; note that solving the rope solution is itself not counted as relevant exploration). Moreover, the ropers' HOI was 29.7% (and significantly) higher than that of non-ropers (χ^2_{ML} =4.06, P<0.05).

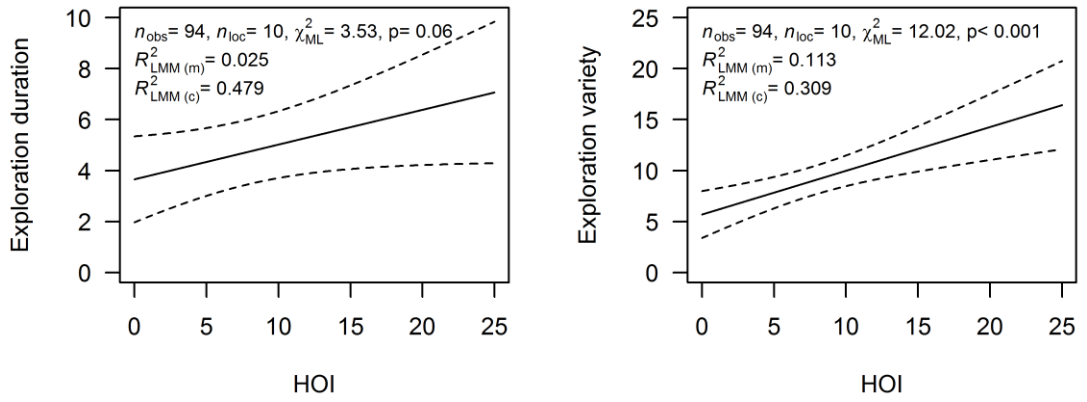

Figure 5. The relationships between the human orientation index (HOI) and exploration behaviour showed significant dependencies in Linear-Mixed-Effect-Models (LMM) that controlled for repeated observations in each facility. (a) Exploration duration in relation to HOI-index (N_{obs}=94, $N_{location}$=10, $\chi 2^{ML}$ =3.53, $R^2_{LMM(m)}$=0.025, P=0.06). (b) Total variety of exploration actions in relation to the HOI (N_{obs}=94, $N_{location}$=10, $\chi 2^{ML}$ =12.02, $R^2_{LMM(m)}$=0.1113, P <0.001).

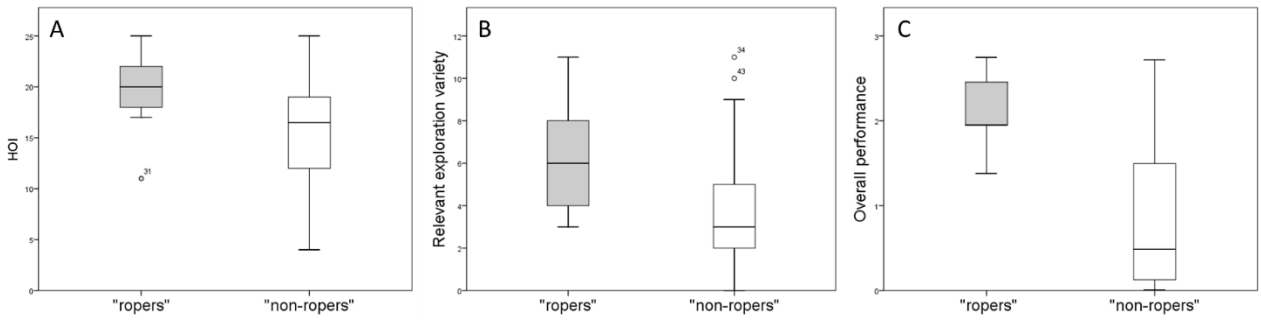

Figure 6: Individuals who solved the more challenging problem of inserting the rope into the L-shaped curved, had significantly higher HOI-index, relevant exploration variety and overall performance, than individuals who failed to find the rope-solution.

5.4.3 Evaluating the human orientation index

Given the large effect of the HOI on exploration style, we examined whether the different background categories determined an individual's human orientation index. 'Wild' individuals strongly diverged from any other category in that they took longer or did not respond at all to the novel food and novel object (Figure 6, Appendix III) and by showing significantly lower HOI values (Kruskal-Wallis test: N=95, P=0.002, Figure 7). However, pairwise comparisons of each background category (controlling for age, sex and species as well as repeated observations from each study location and correction of P-values for multiple comparisons using Tukey) revealed no significant differences in HOI between the background categories (Table 9, Appendix III).

The reaction toward novel humans might also be the result of several other factors, such as a response to any novelty or to social beings (human or orang-utan). Therefore, we also examined the links between HOI and the three novelty response experiments (concerning novel food, novel objects and

novel conspecifics). Results of a Linear Mixed-Effects Model (LMM) evaluated the relation between the HOI and two other novelty response tasks, the novel-object and the novel-food task. The HOI was not explained by the latency to touch either the novel food (B±SD= -0.057±1.12, *df*= 78.83, t= 6.401, P=0.332; Table 5) or the novel toy (B±SD= 0.008±0.02, *df*= 81.9, t= 0.457, P=0.649; Table 5), whereas the latter two were correlated (Spearman's rho: r =0.314, N=98, P=0.002, 2-tailed). Neither did the exploration duration of the novel toy explain the variation in HOI (B±SD= 0.006±0.01, *df*= 81.99, t= 0.584, P=0.561; Table 5). Thus, the HOI did not simply reflect a positive response to novelty per se. To test whether the HOI represents a general interest in social beings, and thereby a higher social motivation in general or whether it describes the interest in humans specifically, we performed an additional social-interest-task with a subset of individuals of one rehabilitation station (N=28, see Method section). The HOI did not seem to measure a general social interest, since the duration spent in close proximity to a novel human did not correlate with the time spent in close proximity to novel conspecifics (Spearman's rho: r =.198, N=28, P=.312, two-tailed).

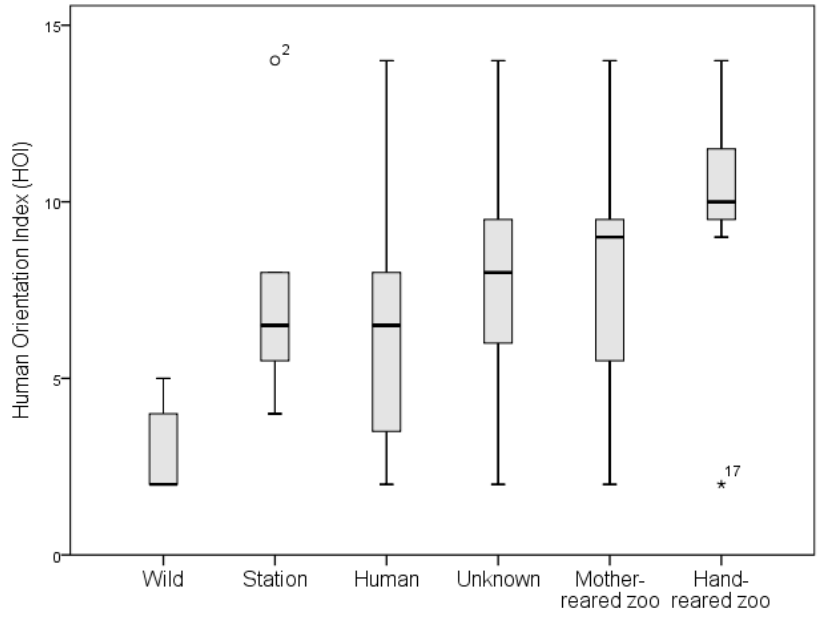

Figure 7: The measured human orientation index for sub-categories of diverse background histories presented with the raw data.

Table 5: Linear Mixed-Effects model of the human orientation index controlling for repeated observations on each facility.

	Estimate	*Std. Error*	*df*	*t value*	*P value*
(Intercept)	15.59252	1.63461	50.76	9.539	<0.001***
Novel food					
Latency touch	-0.13721	0.11044	79.98	-1.242	0.218
Latency taste	0.0161	0.04416	77.49	0.365	0.716
Novel Toy					
Latency touch	0.01408	0.03946	79.74	0.357	0.722
Exploration duration	0.0215	0.01677	79.99	1.282	0.204

5.5 Discussion

This study represents one of the largest systematic individual-level comparisons of cognitive tool-using abilities in apes, involving 13 different captive groups in both zoos and rehabilitation stations in which none of the individuals were deprived or enculturated. As expected, the latency to touch novel food or objects, and thus reduced neophobia, was an important independent predictor of task performance (Table 4), as has been found in other studies (Auersperg *et al*., 2011; Benson-Amram & Holekamp, 2012; Cauchard *et al*., 2013; Sol *et al*., 2012). However, we also found that variation in problem-solving skills in the honey tool-task was equally predicted by persistent and varied explorative behaviour, which in turn was highly influenced by the orangutans' psychological orientation as assessed with the human orientation index, HOI (Table 4). We suggest the following biologically most plausible causal cascade, backed up by a series of analyses: Human orientation mainly influenced both the orang-utans' motivation to explore and the nature of their exploration, and consequently affected their understanding of the problem-solving task, and thus their success in solving it.

The reaction towards humans could have several dimensions, other than the mere interest in humans, and our results allowed us to characterize the nature of the Human orientation Index (HOI) in more detail. A high HOI does not simply reflect the expectation of food that is provided regularly by humans, because HOI varied extensively and all these orang-utans depended on humans for their food. The different background categories also showed higher variability in their HOI than in their novelty response (Figure 7 and Figure 8, Appendix III). Moreover, if it were mere food expectation, variation in HOI should be associated with caretakers that provide the daily food supply rather than random strangers. Finally, the HOI does not reflect general novelty response or general social interest, as it was not correlated with the approach latency to novel food nor objects (Table 5), nor with interest in novel conspecifics. Therefore the effect was human-specific and increased the motivation to explore, expressed as increased duration and variety of exploration (Figure 5a and 5b).

The HOI thus captures a fundamental psychological change that is induced by human contact. The different background categories overlapped largely in their HOI (Table 9, Appendix III), implying that each individual's specific nature and experience of human contact is more influential than the human exposure time per se. However, our sample included a few wild individuals who had spent their whole immature period in natural habitat and showed very low human orientation compared to most other conspecifics housed in zoos and rehabilitation stations, independent of the time they had spent at the station (Figure 7). This indicates that the change caused by humans can only happen at an early age, suggesting a sensitive period for social inputs. Since this kind of psychological orientation is absent in

nature (Forss *et al*., 2015), we can ask which natural process is being mimicked or modified by human contact. The answer is remarkably simple: humans replace the role of the mother and other conspecific experts, and the rich variety of artefacts provided by humans enriches their physical environment. In their natural niche, orangutans as well as other primates are prone to attend to their mother and other expert conspecifics and learn necessary skills socially (Lonsdorf, 2006; Humle *et al*., 2009; Jaeggi *et al*., 2010; van de Waal *et al*., 2013; Schuppli *et al*., 2016). Exploration plays a crucial role in skill acquisition in the wild, but virtually all exploration is socially facilitated, allowing orangutans to overcome intrinsic neophobia (Forss *et al*., 2015).

Given the identification of human orientation, rather than rearing conditions, as the key determinant of cognitive ability in captive apes, it makes sense to revisit the role of deprivation and enculturation. Because deprivation involves the complete loss of any role models, whereas enculturation involves the presence of far richer social inputs by more actively engaged role models than under normal conditions, one could argue that the degree of human orientation may largely explain the whole spectrum of cognitive performance among great apes. This perspective also explains why enculturated apes outperform others not just in socio-cognitive skills, but also in physical cognitive skills (Rumbaugh & Washburn, 2003; Bard *et al*., 2014).

The social triggering of the engagement with artefacts is highly influential in human child development (Tomasello, 1999; Bard & Leavens, 2009). Studies within the field of comparative psychology have documented non-human primates' tendency to attend to humans (Call & Tomasello, 1996; Hirata *et al*., 2009) and acknowledged the improvement in learning cognitive tasks due to human contact in captive settings (Harlow, 1949; Rumbaugh & Pate, 2014). Systematic species comparisons of primates' attention structure toward humans are rare. Nonetheless, in 1916, Yerkes already suggested that the qualitatively better cognitive performance of an orang-utan compared to monkeys was due to the ape's social attention to human actions. Our results thus support previous suggestions (Shumaker *et al*., 2011; Russon & Galdikas, 1993; Byrne & Russon, 1998) that early exposure to humans and human artefacts presents a broader range of opportunities for exploration resulting in increased innovativeness in captive apes. Over time, the accumulating experience resulting from attention to humans leads to improved problem-solving ability, provided the exposure to humans is early in life. In conclusion, human orientation at least partly explains the phenomenon that captive primates that are exposed to both conspecific and human role models experience increased opportunities for socially induced exploration and learning (cf. Bering, 2004).

Our detailed analyses revealed that the HOI influenced an individual's duration and especially its variety of exploration (Figure 5a and 5b), which subsequently explained cognitive performance (Figure 3 and Figure 4a and 4b). Previous studies on hyenas (Benson-Amram & Holekamp, 2012) and birds (Griffin & Guez, 2014) have also reported that the diversity of exploration actions influences

innovativeness and problem-solving skills. However, in our study, individuals with a strong human orientation were more successful in the task, not only through their exploration diversity, but also by focusing on the relevant parts of the apparatus (Figure 3), implying that they were better at recognizing the actual challenge presented in the honey tool-task. Importantly, these parts were relevant not because they directly led to the solution, but rather because exploration of these parts improved the animals' understanding of the physical properties of the problem. For example, individuals that traced the honey channel from the outside of the glass obviously understood that there is honey inside, but were at that time not searching at the correct part of the apparatus, the channel entrance. Similarly, individuals poking with their finger into the curved channel may have gathered information on its length. Exploration can therefore be viewed as latent learning: it allows an animal to gather knowledge of the texture, the material, and the problem itself. Over time, then, individuals with a high HOI will gain more experience, which contributes to their focus on relevant aspects of the problem and hence problem-solving success.

The effects of the HOI on problem-solving success may have been so strong that they masked the effects of other factors. Thus, we found no differences between the two orangutan species (*P. abelii* and *P. pygmaeus*), even though these were found when orang-utans with very similar backgrounds (all mother-reared zoo individuals) were compared on a range of cognitive tasks (Forss *et al*., 2016).

This study documented strong effects of human orientation on problem-solving abilities, through its effects on response to novelty, motivation to explore, exploration persistence and ultimately experience. This finding suggests that it is just as impossible to design culture-free cognitive tests for primates as it is for humans. In this sense, tests of primate cognition are inevitably deeply anthropomorphic. However, once we have controlled for the subjects' human-related histories and given that problem-solving ability is about dealing with unknown, novel problems the variation captured in these tests nonetheless reflects variation in intrinsic cognitive abilities and should be comparable within and across species. Therefore, we suggest the HOI may be a useful tool in standardizing comparisons across primates, especially studies concerning ape subjects with various background and human-related experiences. In future work, we will further disentangle the exact nature and causes of the HOI and address additional problem-solving domains.

5.6 Acknowledgements

We would like to dedicate our warmest thanks to all the collaborating zoos and rehabilitations centers, where we conducted the study: Zoo Dortmund, Twycross Zoo, Durrell Wildlife Trust, Allwetterzoo Münster, Zoo Basel, Apenheul Primate Park, Wolfgang Köhler Primate Center at Leipzig Zoo, Blackpool

Zoo and Paignton Zoo, Nyarung Menteng (BOS), Orangutan Care Center and Quarantine (OCCQ), Sumatran Orangutan Conservation Program (SOCP) – Quarantine and Danau Alo. We thank Andreas Wendl for assisting the data collection in the rehabilitation stations and Anna Schöpfer for helping out with the video coding of the Indonesian sample. We also thank all our male participants representing the unfamiliar human in our experimental test. In particular, from my side I would like to thank all the animal caretakers at each zoo for their helpful support throughout the experimental process as well as Ilona Schappert, Charlotte McDonald, Gordon Hunt, Simone Schehka, Adrian Baumeyer, Thomas Bionda, Laura Salanki, Matthew Webb, Johannes Grossmann, Sebastian Schütte, Raik Pieszek and Hanna Petschauer for showing great interest and cooperation in pursuing this project. Finally, we would like to address my gratefulness to Judith Burkart and Katja Liebal for their contributions on developing the test set ups during the project planning.

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Conclusion & Outlook

Although humans have evolved specialized adaptations making us a culture-dependent species, this thesis examined the idea that processes underlying cultural learning are more widely distributed and impact cognitive abilities in nonhuman primates. I therefore conducted four projects to test the presence of culturally constructed intelligence in orangutans.

First, we saw that despite being a species acknowledged for its explorative and innovative tendencies, orangutans are ironically not naturally curious toward novelty and in fact strongly avoid it. Thus, even though innovations are the building blocks of what we define as orangutan culture, individuals do not boldly explore novel things and rarely invent under natural conditions. Consequently, the individual pathway, assuming innovations to appear from intrinsic curiosity expressed through novelty response, can be rejected in this particular case. Instead, I suggest that innovations may arise because the acquisition of skills through social learning can occasionally result in modifications of existing innovations. These results are inconsistent with the widespread assumption that novelty response is a common and straightforward pathway to animal innovation. The finding prompted me to do a literature review (*Chapter 3*), which suggests that social (cultural) species prefer attending to social information if available, when confronted with novelty. In slow paced life-history species - depending on learning - this effect may even depend on specific experts or role models. This can explain why in natural conditions innovations are relatively rarely made. Furthermore, it implies that innovations are retained as a consequence of effective social learning ability. In long-lived species characterized by an extended developmental phase - like the orangutans - socially protected learning represents an adaptation through which risks can be avoided. In consequence investment in novelty exploration does not provide additional fitness advantages, whereas selection on learning efficiency is highly beneficial.

On the contrary, the very same species, which have evolved to effectively learn skills from conspecifics rather than engage in risky independent exploration, can be made to express the opposite behavior – novelty-based curiosity – once the constraints of risk are removed and environmental conditions allow for it. One such case is when animals are kept in artificial and risk-free habitats, like the enriched conditions of captivity provided by modern zoos. Captive animals experience different environments from those of conspecifics in natural habitats, which can affect their cognition – a process that can give rise to the *captivity effect*, the phenomenon that captive animals show greatly different psychological attitudes and cognitive abilities compared with their wild counterparts.

Secondly, by investigating the effect of captive habitats, I found that in some species captivity can reduce the default state of evolved neophobia (*Chapter 2 & 3*). Due to a risk-free and safe habitat captive animals experience a reduced cognitive load, allowing for exploration to thrive once neophobia

is suppressed. This is especially pronounced in species where exploration tendency is intrinsically high and somewhat socially induced – like the orangutans. Because most cognitive studies assessing innovativeness have so far been conducted solely in captive settings, it is easily assumed that large-brained species like great apes are highly curious and innovative, although this paradoxically represents the exceptional state where animals can afford to invest in curiosity. Consequently, looking at a species' innovativeness only in captivity can lead to misleading conclusions. Unfortunately, the opposite of only considering cognitive abilities as revealed by field measurements of innovativeness in natural habitat runs the risk of measuring neophobia only.

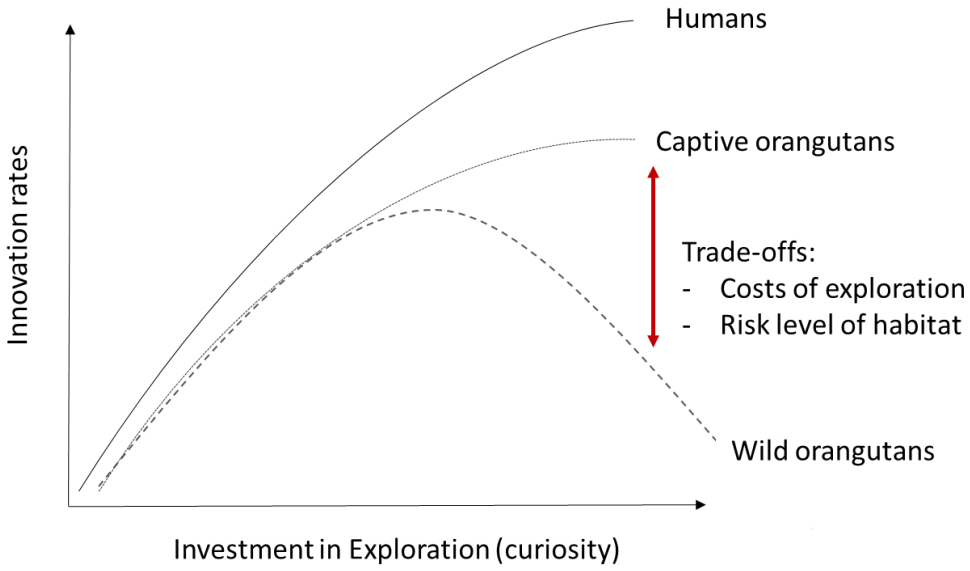

Figure 1: Illustrative framework of innovativeness. In natural habitats investment in exploration, (especially of novelty) is constrained by trade-offs linked to costs of potential predation risk, poisonous food intake as well as opportunity costs linked to time and energy. As a result innovation rates in natural habitats remain relatively low. In contrast, captive habitats lack the cost of investment in exploration allowing for higher innovation tendencies. These are additionally boosted by the effect of intense social cues. This effect of reduced risk linked to a captive existence illustrate the conditions of the creative nice of humans.

The findings from this thesis also show that the effects of a life in captivity is more than loss of neophobia - especially in great apes - who are adapted to learn from others and therefore also can attend to humans as additional role models. Accordingly their intensified social environment alters attentiveness, causing further cognitive changes. Thus as a third factor I showed that among orangutans, the specific social stimulus provided by humans permanently changes their attitudes toward novel problem-solving task, resulting in better physical cognitive skills. *Chapter 5* reports huge variation in problem-solving ability, which in our model was best predicted by human orientation, which in turn was measured with an independent test assessing attentiveness to an unfamiliar human. Beyond improved actual performance, individuals with higher human orientation were also more curious and creative: they explored the task longer and used more variable exploratory actions while doing so. Thus, the documented captivity effect and individual variation in cognitive performance in orangutans represent a change in attention structure caused by the social component of human exposure and the experiences associated with this. As great apes exhibit high a potential for curiosity

and creativity, only certain conditions facilitate such behavior, implying that creative behavior is an evolutionary byproduct expressed when risk constraints are absent. This may help us understand some fundamental perspectives on why humans have become creative and the results are incorporated in a recent review on the phylogeny of creativity by van Schaik *et al*. (2016). One could therefore argue that the results of the captivity effect on ape cognition documented here reflect historical changes that led to the niche of modern human foragers. As our species overcame predation pressures, a combination of reduced cognitive load and pronounced cultural learning may have promoted conditions ideal for creative exploration (van Schaik *et al*., 2016). It would be valuable to investigate multiple large-brained and cultural species to test the generality of this conclusion.

Because cognitive abilities in apes are highly plastic and influenced by experiences, potential intra-individual variation (the reaction norm) is broad and context dependent. This range of plasticity – in typical data sets usually regarded as some sort of "noise"– challenges comparisons between species. Based upon the findings of my dissertation, I would like to emphasize the importance of considering experience effects, as we did by measuring a subject's human orientation in chapter 5. This may be especially important when performing comparative studies not only on great apes, but in any species where skills are acquired through inputs during development. Thus when considering primate cognition, the introduced HOI-measurement describes a continuous process, of which the end point is enculturation. Hence, among captive apes cognitive skills may never be culture-free due to the effects of individuals´ specific experiences. It remains to be discovered whether this impact of human attentiveness is strong enough to outweigh species differences when evolutionary distances become greater than the two closely related species of orangutans measured so far. When the evolutionary gap between species are larger, like chimpanzees and bonobos, species-specific cognitive predispositions are more distinct, which provides interesting conditions to test for the strength of developmentally constructed experience effects.

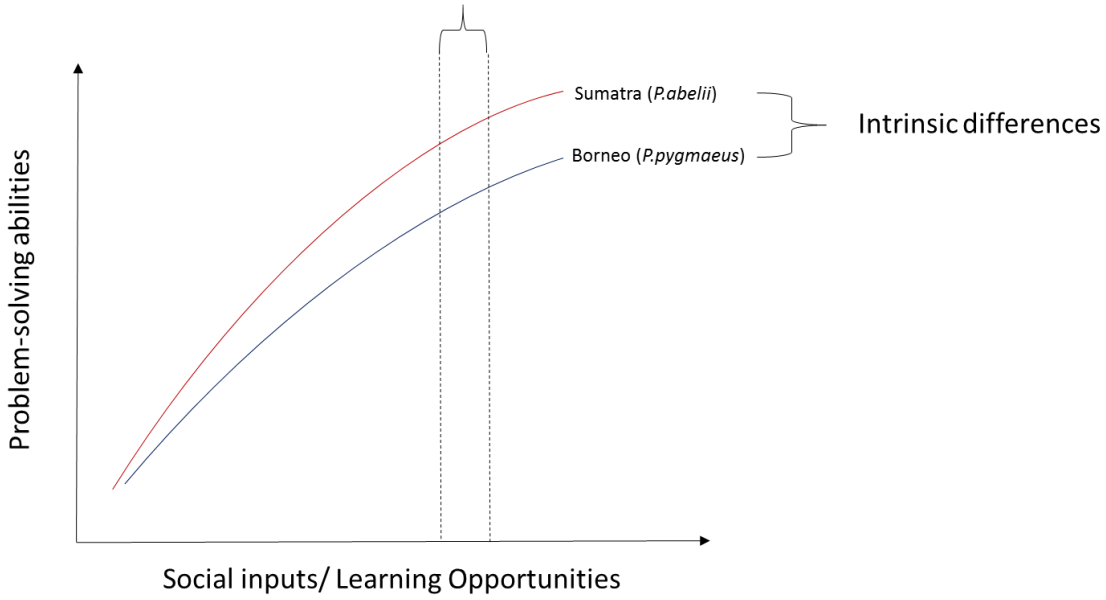

Figure 2: Orangutan cognitive abilities are strongly related to the quantity and quality of social inputs and learning experiences an individual is exposed to. Consequently, intrinsic differences between the two Pongo species, resulting from different evolutionary histories in learning opportunities, emerge when the experience effect is controlled for.

Since experience effects - caused by human exposure - were highly influential on orangutan problem-solving skills, an honest comparison of cognitive abilities between the two *Pongo* species required a sample of individuals who have experienced identical social and environmental inputs. As a final goal, I delivered the first empirical test of the *Cultural Intelligence Hypothesis* in a non-human taxon by comparing a sample containing only standard mother-reared individuals, with similar human orientation values, living in highly similar zoo environments. Here intrinsic differences in cognitive performance appeared: Sumatran orangutans outperformed the Borneans. Thus the combination of more advanced skill repertoires and frequencies for social learning opportunities have over an evolutionary time scale produced cognitive differences between the two *Pongo* species. We saw that not only do they differ in physical problem-solving performance, but also in underlying mechanisms such as inhibitory control and caution, traits that may very well be under selection when selection is on the efficiency of social skill transmission, and thus crucial for cultural learning to take place. More generally, the traditional benefit hypotheses for the evolution of intelligence, such as the social brain hypothesis (Byrne & Whiten, 1988; Dunbar & Shultz, 2007) or the technical intelligence hypothesis (Byrne, 1997), both face the problem of grade shifts, i.e. that different lineages show major differences in intelligence in spite of similar social or technical challenges (Holekamp 2007; van Schaik *et al*., 2012). The cultural intelligence hypothesis, which basically argues that where learning is more efficient intelligence can be enhanced, may therefore be essential to complement the explanatory power of these benefit hypotheses.

All in all, in orangutans – as in humans – behaviors that require intelligence are constructed during development mainly depending on the social input an individual is exposed to and thus highly sensitive to various experiences. When experience effects are kept as constant as possible, we can make species differences in cognitive capacity visible. The results from my dissertation therefore illustrate the two levels of cultural intelligence: the magnitude of individual experiences extracted from the social environment and the evolutionary outcomes of socially constructed intelligence.

Appendix I: Tables to chapter 3

Table 1: Social facilitation effect; individuals tested alone versus social condition

Species	Test paradigm	Test setting	Social condition reduce neophobia	Kin effect	Remark	Study
Sturnus vulgaris starling	Novel object/ A	Captive	No		Individuals tested alone were not more neophobic than those tested with their group	*Apfelbeck & Raess 2008*
Acridotheres tristis mynah	Novel object/ A	Captive	No		When tested with conspecifics birds delayed approach to a novel object relative to when alone	*Griffin et al. 2013*
Quiscalus lugubris carib grackle	Novel P-S/ D	Captive	No		Birds took longer to approach problem-solving apparatus in social condition	*Overington et al. 2009*
Corvus corax raven	Novel object/ B	Captive	No	Yes	Birds approached novel objects faster when alone than in social condition and approached faster when tested with siblings compared to non-kin	*Stöwe et al. 2006a* *Stöwe et al. 2006b*
Perca fluviatilis perch	Novel food/ C	Captive	Yes		Presence of trained demonstrator influenced consumption of novel food	*Magnhagen & staffan 2003*
Taeniopygia guttata Zebra finch	Novel object/ A	Captive	Yes		Birds in flocks were less neophobic than solitary birds	*Coleman & Mellgren 1994*
Melopsittacus undulatus parakeet	Novel object/ A	Captive	Yes		Reduced approach latencies in social condition	*Soma & Hasegawa 2004*
Pachyuromys duprasi gerbil	Novel food/ C	Captive	Yes		Subjects reduced food neophobia in presence of trained demonstrator	*Forkman 1991*
Canis lupus wolf	Novel object/ B	Captive	Yes	Yes	Presence of conspecifics, especially kin, reduced latencies toward novel objects	*Moretti et al. 2015*
Canis familiaris dog	Novel object/ B	Captive	Yes	Yes	Presence of conspecifics, especially kin, reduced latencies toward novel objects	*Moretti et al. 2015*

Callithrix jacchus marmoset	Novel food/ C	Captive	Yes	Juvenile marmosets showed higher food neophobia when tested alone than in group condition	*Yamamoto & Lopes 2004 Voelkl et al. 2006*
Cebus apella capuchin	Novel food/ C	Captive	Yes	Consumption of novel food increased in social setting compared to alone condition	*Visalberghi & Fragaszy 1995 Visalberghi & Addessi 2000*
Crocuta crocuta hyena	Novel P-S/ D	Wild	Yes	Presence of conspecific at apparatus reduced approach latencies	*Benson-Amram & Holekamp 2012*

Table 2: Novelty response examined in a group setting where novelty is assumed equally unfamiliar to all subjects

Species	Test paradigm	Setting	Approach latency/ initial neophobia	Study
Corvus corone corone crow	Novel food/ C	Wild	Dominant males < other age/sex classes	*Chiarati et al. 2012*
Suricata suricatta meerkat	Novel P-S/ D	Wild	Juveniles < Adults	*Thornton & Samson 2012*
Rhinopithecus roxellana snub-nosed monkey	Novel object/ A	Wild	Immatures & Adults < infants	*Fu et al. 2013*
Macaca fuscata Japanese macaque	Novel object/ B	Wild	Juveniles < Adults	*Menzel 1966*
Papio anubis olive baboon	Novel P-S/ D	Wild	Juvenile male < rest of group	*Laidre 2007*
Papio ursinus chacma baboon	Novel object/ B	Wild	No age effect	*Bergman & Kitchen 2009*
Theropithecus gelada gelada	Novel object/ B	Wild	No age effect	*Bergman & Kitchen 2009*
Cebus apella capuchin	Novel food/ C	Wild	Immatures < Adults	*Visalberghi et al. 2003*

Cebus apella capuchin	Novel object/ B	Wild	No age effect	*Visalberghi et al. 2003*
Pan troglodytes chimpanzee	Novel food/ C	Wild	Immatures < Infants, Adults	*Biro et al. 2003*
Crocuta crocuta hyena	Novel P-S/ D	Wild	Juveniles < Adults	*Benson-Amram et al. 2013*
Crocuta crocuta hyena	Novel P-S/ D	Captive	Adults < Juveniles	*Benson-Amram et al. 2013*
Canis lupus wolf	Novel Object/ B	Captive	Older individuals < Younger individuals	*Moretti et al. 2015*
Canis familiaris dog	Novel Object/ B	Captive	Older individuals < Younger individuals	*Moretti et al. 2015*
Erythrura gouldiae Gouldian finch	Novel object/ A & B	Captive	Older birds < younger birds (relative age)	*Mettke-Hofmann 2012*
Callicebus moloch titi monkey	Novel Object/ B	Captive	Juveniles < Adults	*Mayeaux & Mason 1998*
Callicebus moloch titi monkey	Novel Food/ C	Captive	No age effect	*Mayeaux & Mason 1998*
Callithrix spp marmoset	Novel P-S/ D	Captive	No age effect	*Kendal et al. 2005*
Saguinus fuscicollis tamarin	Novel object/ B	Captive	Adult male/ older offspring < other	*Menzel & Menzel 1979*
Cebus apella capuchin	Novel object/ B	Captive	Males < Females, Young adults, Juveniles < Adult, Infants	*Visalberghi 1988*

Papio papio Guinea baboon	Novel object/ B	Captive	Juveniles & Males < Females	*Joubert & Vauclair 1985*
Daubentonia madagascariensis Aye-aye	Novel food/ C	Captive	Mothers < Infants	*Krakauer 2005*
Cercopithecus a. sabaeus vervet monkey	Novel object/ A	Captive	Juveniles < Mothers < Infants	*Fairbanks and McGuire 1993, Fairbanks 1993*

Table 3: Intrinsic tendencies; subjects tested alone excluding social effect

Species	Test paradigm	Setting	Fastest approach/ ingestion latencies	Study
Canis lupus dog	Novel object/ A	Captive	Adults	*Moretti et al. 2015*
Canis familiaris wolf	Novel object/ A	Captive	Adults	*Moretti et al. 2015*
Callithrix jacchus marmoset	Novel food/ C	Captive	Adults	*Yamamoto & Lopes 2004*
Cebus apella capuchin	Novel food/ C	Captive	No age effect	*Visalberghi & Addessi 2000*
Milvago chimango falcon	Novel object/ A	Captive	Juveniles	*Biondi et al. 2010*
Pongo spp. orangutan	Novel object/ B	Wild	Adolescents	*Forss et al. 2015*
Equus caballus horse	Novel object/ B	Captive	24 week old less neophobic than 3- and 12 week old foals	*Lansade & Bouissou 2007*

Table 4: Asymmetry in knowledge and impact of specific social cues

Species	Test paradigm	Social cue reduce neophobia	Influential social source	Comparison	Study
Salmo salar Atlantic salmon	Novel food/ C	Yes	Trained conspecific	Influence of trained versus untrained conspecific	*Brown & Laland 2002*
Gallus spadieceius red jungle fowl	Novel food/ C	Yes	Video of conspecific	Video showing conspecifics feeding on different food dishes and general activities near food	*McQuoid & Galef 1993*
Gallus domesticus domesticated fowl	Novel food/ C	Yes	Trained conspecific	Demonstrator's disgust response versus demonstrator preference	*Sherwin et al. 2002*
Corvus corax raven	Novel object/ A	Yes	Human observer	Ravens would approach objects faster if observing human caretaker providing the objects. (No control reported)	*Heinrich 1988*
Rhabdomys pumilio striped mouse	Novel food/ C	Yes	Mother	Mothers versus fathers as demonstrators	*Rymer et al. 2008*
Sus domesticus pig	Novel food/ C	Yes	Demonstrator familiar	Demonstrator from same versus different pen	*Figueroa et al. 2013*
Eulemur macaco macaco lemur	Novel food/ C	Yes	Dominant female	Dominant female present versus absent	*Gosset & Roeder 2001*
Macaca mulatta macaque	Novel food/ C	Yes	Human observer	Food found without human present versus food given by human observer	*Johnson 2000a*
Pan troglodytes chimpanzee	Novel food/ C	Yes	Mother	Familiar food versus novel food. Mothers influenced ingestion of novel but not familiar foods	*Ueno & Matsuzawa 2004*
Homo sapiens human	Novel food/ C	Yes	Familiar adult	Three conditions: A. adult model not eating, B. adult model eating different food and C. adult model eating same food	*Addessi et al. 2005*

Table 5: Species where a captivity effect of neophobia has been examined

Species	Test paradigm	Effect of human rearing	Reduced neophobia in captivity	Study
Corvus corax raven	Novel food	Yes	Yes	*Heinrich 1988, Heinrich et al. 1995a*
Amazona amazonica parrot	Novel object	Yes	Yes	*Fox and Millam 2004*
Pica pica Magpie	Novel object		Yes	*Shephard et al. 2015*
Mus m. domesticus Mouse	Novel food		Yes	*Kronenberger and Médioni 1985*
Rattus norvegicus rat	Novel food		Yes	*Barnett 1958*
Rattus norvegicus rat	Novel object		Yes	*Tanas and Pisual 2010*
Vulpes velox fox	Novel object		Yes	*Bremner-Harrison et al. 2004*
Crocuta crocuta hyena	Novel P-S apparatus		Yes	*Benson-Amram et al. 2013*
Cebus apella capuchin	Novel object + Novel food		Yes	*Visalberghi et al. 2003*
Papio papio baboon	Novel P-S apparatus		Yes	*Laidre 2007, Joubert & Vauclair 1985*
Pongo abelii orangutan	Novel object	Yes	Yes	*Forss et al. 2015*

Appendix II: Additional figures & tables for chapter 4

Table 2: List of all subjects participating in the cognitive tasks.

Subject	Species	Age at testing	Current Zoo	# Zoos lived in	Sex
Ito	*Pongo pygmaeus*	6	Allwetterzoo Münster	1	Male
Pongo	*Pongo pygmaeus*	15	Allwetterzoo Münster	2	Male
Amos	*Pongo pygmaeus*	13	Apenheul	2	Male
Radja	*Pongo pygmaeus*	52	Apenheul	3	Female
Silvia	*Pongo pygmaeus*	49	Apenheul	2	Female
Jose	*Pongo pygmaeus*	21	Apenheul	2	Female
Sandakan	*Pongo pygmaeus*	32	Apenheul	3	Female
Samboja	*Pongo pygmaeus*	9	Apenheul	1	Female
Willie	*Pongo pygmaeus*	12	Apenheul	1	Male
Batu	*Pongo pygmaeus*	14	Twycross zoo	2	Male
Summer	*Pongo pygmaeus*	13	Blackpool zoo	1	Female
Cherie	*Pongo pygmaeus*	18	Blackpool zoo	1	Female
Mali	*Pongo pygmaeus*	20	Paignton zoo	2	Female
Gambira	*Pongo pygmaeus*	18	Paignton zoo	1	Female
Anette	*Pongo abelii*	30	Durrell wildlife trust	3	Female
Jaya	*Pongo abelii*	9	Durrell wildlife trust	1	Male
Dagu	*Pongo abelii*	28	Durrell wildlife trust	5	Male
Dana	*Pongo abelii*	25	Durrell wildlife trust	3	Female
Gina	*Pongo abelii*	49	Durrell wildlife trust	1	Female
Budi	*Pongo abelii*	8	Basel zoo	2	Male
Maia	*Pongo abelii*	5	Basel zoo	2	Female
Kila	*Pongo abelii*	13	Basel zoo	2	Female
Vendel	*Pongo abelii*	13	Basel zoo	4	Male
Djamuna	*Pongo abelii*	13	Dortmund zoo	3	Female
Toba	*Pongo abelii*	18	Dortmund zoo	2	Female
Tao	*Pongo abelii*	8	Dortmund zoo	2	Female
Walter	*Pongo abelii*	23	Dortmund zoo	4	Male
Dokana	*Pongo abelii*	25	Leipzig zoo	4	Female
Padana	*Pongo abelii*	16	Leipzig zoo	1	Female
Pini	*Pongo abelii*	25	Leipzig zoo	1	Female
Raja	*Pongo abelii*	13	Leipzig zoo	1	Female
Tanah	*Pongo abelii*	5	Leipzig zoo	1	Female
Suaq	*Pongo abelii*	5	Leipzig zoo	1	Male

Table 3: Zoos and housing conditions where data was collected

Zoo	Species	Time of study	Group size	Outdoor Enclosure	Sleeping quarters	# permanent enrichment devices
Twycross zoo	*Pongo pygmaeus*	January-February 2013	4	Yes	Yes	1
Allwetter zoo münster	*Pongo pygmaeus*	April- May 2013	6	Yes	Yes	3
Apenheul Primate Park	*Pongo pygmaeus*	January-February 2014	12	Yes	Yes	2
Blackpool zoo	*Pongo pygmaeus*	January 2015	4	Yes	Yes	1
Paignton zoo	*Pongo pygmaeus*	February 2015	5	Yes	Yes	1
Dortmund zoo	*Pongo abelii*	November-December 2012	6	No	Yes	1
Durrell Wildlife Trust	*Pongo abelii*	March 2013	6	Yes	Yes	3
Basel zoo	*Pongo abelii*	November 2013	6	Yes	Yes	1
Leipzig zoo	*Pongo abelii*	March 2014	10	Yes	Yes	2

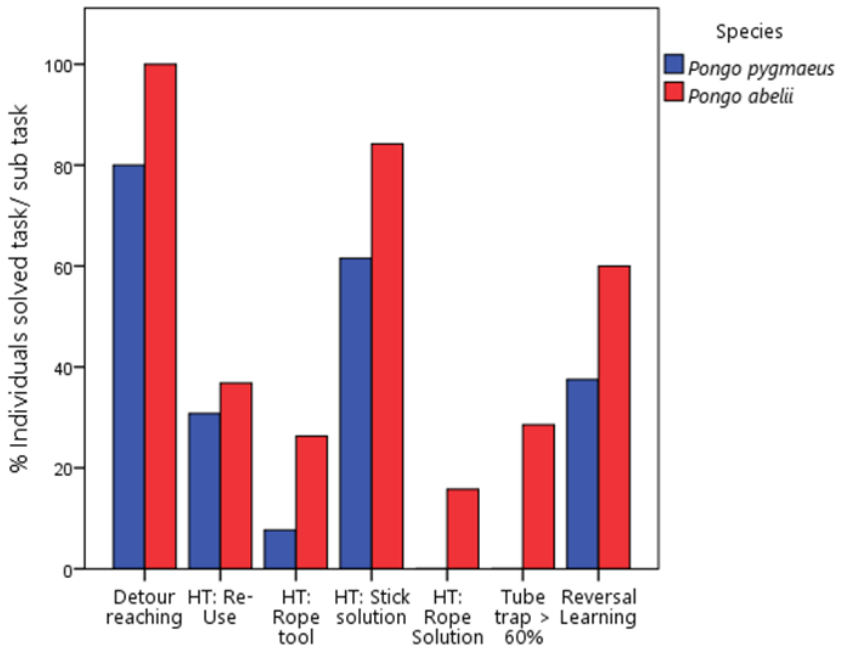

Figure 10: Percentage of subjects that successfully solved each task. Sumatran species (*Pongo abelii*) would perform significantly better than the Bornean species throughout all tasks (*Pongo pygmaeus*) (Wilcoxon signed rank test: $N_{P.abelii}=7$, $N_{P.pygmaeus}=7$, $Z=-2.366$, $P=0.018$).

In addition, I evaluated the level of difficulty for each task by looking at how many out of all tested zoo orangutans, successfully solved a task or not and performed supplementary analyses on the data set including the assessment of task difficulty. The task measurements were ranked in following order ranging from the easiest to the most demanding task: (1) Detour reaching (N=29; correctly solved: 26/29=90%) (2) Visible honey trap; solution straight trap (N=42; correctly solved: 30/42=71%) (3) Reversal learning (N=29; learned reverse: 12/29=41%) (4) Visible honey trap; re-use of stick (N=42; used given stick: 13/42=31%) (5) Visible honey trap; use rope as a tool (N=42; tried rope as tool: 9/42=21%) (6) Visible honey trap; solution L-shaped trap (N=42; correctly solved: 5/42=12%) (7) Tube trap task; solved more than 60% of tubes correct (N=31; correctly solved: 4/31=13%). In a binomial generalized linear mixed model (GLMM) the data was analyzed based upon weather each individual solved or failed a task, including species as a random factor and controlling for age, sex, and group size. Because some zoo housed apes are moved in between zoos during their lifetime, they may differ in their experiences and thus we also included the number of zoos a subject has been housed as a random factor into our model. The model was highly significant (χ2ML=63.83, N_{total}=196, N_{ind}=33, P<0.001) and showed a substantial species difference in task performance (N_{total}=196, N_{ind}=33, SE=0.59, Z=2.67, P=0.0075, Figure 11). We also found a negative trend of number of zoos an individual had lived on task performance (N_{total}=196, N_{ind}=33, B=-0.493, SE=0.25, Z=-1.88, P=0.0601). Compellingly, even if we tested for multiple tasks and measurements varying in difficulty, there was no single task were the Bornean species would show higher percentage of performance than the Sumatran species, which exceeded in all tasks.

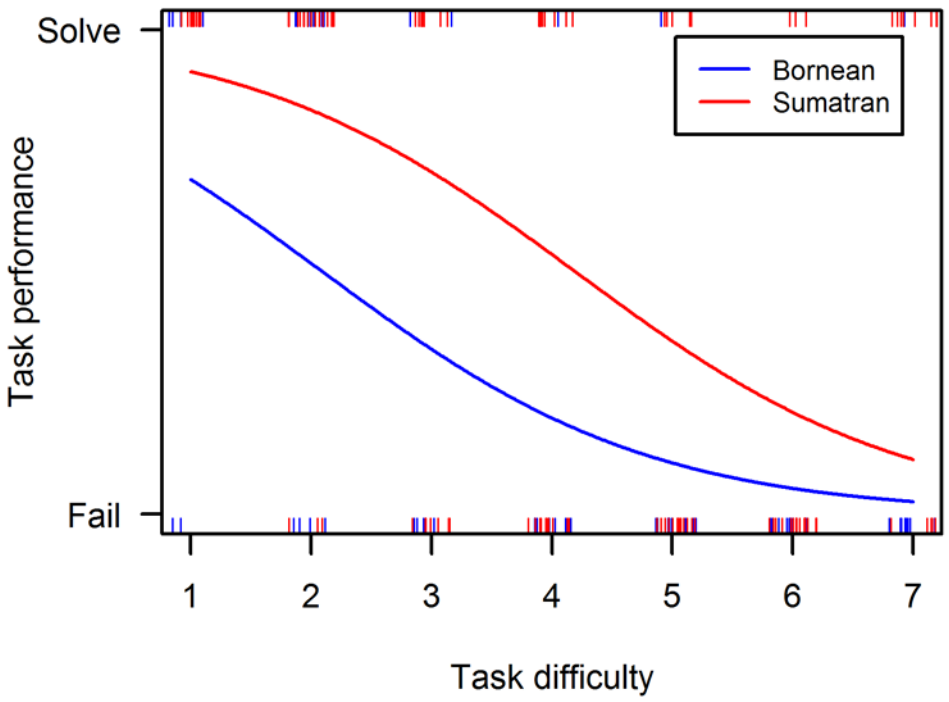

Figure 11: Overall task performance over the different tasks listed according to difficulties. Performance of each subject is plotted as solved or failed, *Pongo abelii* is assigned in red and *Pongo pygmaeus* in blue.

Table 3: Output from the binomial generalized linear mixed model (GLMM) showing species differences in task performance.

	B	SE	z-value	P
Intercept	1.481	1.06	1.39	0.1634
Task difficulty	-0.750	0.13	-5.91	0.0000
Species				
Pongo pygmaeus	-	-	-	-
Pongo abelii	1.576	0.59	2.67	0.0075
Sex				
Female	-	-	-	-
Male	0.487	0.58	0.83	0.4043
Age	0.008	0.02	0.34	0.7354
Number of zoos	-0.478	0.25	-1.88	0.0601
Group size	0.113	0.10	1.12	0.2632
	N_{obs}= 196 on 33 individuals from 9 zoos; X^2_{ML}= 63.83, p< 0.0001			

Appendix III: Additional figures & tables for chapter 5

Table 5: Parameter estimates from a binomial GLMM, predicting the probability of an animal solving the task when excluding independent variables for the novelty response tests.

Generalized Linear Mixed Model of overall performance in the honey tool-task.

Parameter estimates from a binomial GLMM, predicting the probability of an animal solving the task.

	B	***SE***	***Z***	***p value***
Human Orientation Index	0.243	0.09	2.679	**0.007 ****
Age	-0.018	0.03	-0.582	0.561
SEX (male)	-0.619	0.53	-1.158	0.247
Species (Sumatra)	0.295	0.60	0.484	0.628
Background				
Wild vs. Rest	-0.212	0.24	-0.890	0.373
Rehab vs. Zoo	-0.131	0.30	-0.436	0.663
Unknown vs. Rehab.Rest	0.160	0.22	0.730	0.466
Human vs. Station (within rehabilitation station)	-0.489	0.52	-0.933	0.351
Mother vs. Hand (within zoo)	0.383	0.52	0.573	0.465
Accessibility (trend analysis)				
Linear	1.211	0.87	1.395	0.163
Quadratic	1.209	0.97	1.249	0.212
Cubic	0.099	0.97	0.103	0.918
Sub-task (trend analysis)				
Linear	-5.046	0.72	-6.981	**<0.001*****
Quadratic	1.512	0.42	3.567	**<0.001*****
Cubic	-0.149	0.33	-0.457	0.648

Note: Analysis included 94 individuals in 10 different zoos/rehab stations, totalling 376 observations, χ^2_{ML}= 220.60, P< 0.001

Table 6: Parameter estimates from a binomial GLMM, predicting the probability of an animal solving the task. Analysis without the HOI.

General Linear Mixed Model of overall performance in the honey tool-task.

Parameter estimates from a binomial GLMM, predicting the probability of an animal solving the task.

	B	***SE***	***Z***	***p value***
(Intercept)	-0.609	0.91	-0.670	0.503
Age	0.001	0.03	0.023	0.981
SEX (male)	-0.638	0.51	-1.252	0.210
Species (Sumatra)	0.186	0.56	0.332	0.740
<u>Background</u>				
Wild vs. Rest	-0.360	0.22	-1.604	0.109
Rehab vs. Zoo	-0.115	0.26	-0.447	0.655
Unknown vs. Rehab.Rest	0.221	0.21	1.041	0.298
Human vs. Station (within rehabilitation station)	-0.613	0.51	-1.201	0.230
Mother vs. Hand (within zoo)	0.157	0.41	0.381	0.704
<u>Accessibility (trend analysis)</u>				
Linear	0.910	0.81	1.118	0.263
Quadratic	1.499	0.83	1.803	0.071 .
Cubic	0.120	0.82	0.146	0.884
<u>Sub-task (trend analysis)</u>				
Linear	-4.905	0.66	-7.478	**<0.001 *****
Quadratic	1.509	0.39	3.830	**<0.001 *****
Cubic	0.036	0.31	0.118	0.906

Note: The model is controlling for repeated observations on each facility and individual. The performance in the honey tool-task was binary measured. The Analysis included 103 individuals in 12 different zoos/rehab stations, totalling 412 observations, χ^2= 236.43, *P*< 0.001

Table 7: Detailed list of all different exploration actions coded as relevant and irrelevant exploration during the time an individual engaged with the honey tool-task.

Relevant Exploration Actions	Irrelevant Exploration Actions
Insert stick into L-shaped channel	Hit (with any body parts) test apparatus or board
Insert finger into L-shaped channel	Hit (with any body parts) table on which apparatus is presented
Insert finger into I-shaped channel	Pull/ Push test apparatus, plexiglas, screws
Insert rope into I-shaped channel	Pull/ Push table or board on which apparatus is presented
Trace/ Poke finger outside glass of either I- or L-shaped channel	Touch test apparatus, plexiglas, screws (elsewhere but channels)
Trace/ Poke stick outside glass of either I- or L-shaped channel	Touch table or board on which apparatus is presented
Tool modification/ manufacture	Poke stick at apparatus, plexiglas, screws (elsewhere but channels)
Insert any other tool than stick or rope into L-shaped channel	Poke stick at board/table on which apparatus is presented
Insert any other tool than stick or rope into I-shaped channel	Touch sticks on the floor or besides test apparatus
Poke or push stick at opening of L-shaped channel	Touch ropes on the floor or besides test apparatus
Poke or push stick at opening of I-shaped channel	
Poke or push finger at opening of L-shaped channel	
Poke or push finger at opening of I-shaped channel	

Table 8: Linear Mixed-Effects Model of relevant exploration variety controlling for repeated observations on each facility.

	B	***SE***	***df***	***t value***	***p value***
(Intercept)	1.209	1.41	48.66	0.857	0.396
HOI	0.221	0.05	80.07	4.049	**<0.001 *** **
Age	0.014	0.03	80.84	0.414	0.680
SEX (male)	-0.059	0.55	79.52	-0.106	0.916
Species (Sumatra)	0.946	0.87	6.31	1.084	0.318
<u>Background</u>					
Wild vs. Rest	0.162	0.25	75.37	0.652	0.517
Rehab vs. Zoo	0.356	0.33	42.06	1.063	0.294
Unknown vs. Rehab.Rest	0.408	0.23	80.76	1.746	0.085 .
Human vs. Station (within rehabilitation station)	-0.257	0.53	79.81	-0.483	0.630
Mother vs. Hand (within zoo)	0.314	0.58	65.78	0.544	0.589
<u>Accessibility (trend analysis)</u>					
Linear	0.316	1.11	12.64	0.285	0.780
Quadratic	0.467	1.13	23.52	0.411	0.685
Cubic	1.540	1.04	77.21	1.486	0.141

Note: The model is controlling for repeated observations on each facility. The analysis was totalling 94 observations in 10 different zoos/rehab stations, $\chi^2 = 30.91$, $p < .0005$

Table 9: Pairwise comparisons of the Human Orientation Index (HOI) between the different background and rearing categories.

Pairwise comparisons of HOI between different background categories, controlling for age, sex, island and repeated observations from each zoo and rehabilitation station.				
	B	***SE***	***Z***	***p value***
Hand-reared zoo - Station	1.649	2.03	0.814	0.960
Human - Station	-1.452	1.35	-1.078	0.877
Mother-reared zoo - Station	-0.605	1.62	-0.372	0.999
Unknown - Station	-0.279	1.28	-0.217	1.000
Wild - Station	-3.568	2.46	-1.450	0.670
Human – Hand-reared zoo	-3.102	1.82	-1.707	0.497
Mother-reared zoo – Hand-reared zoo	-2.254	1.50	-1.499	0.637
Unknown – Hand-reared zoo	-1.928	1.74	-1.106	0.864
Wild – Hand-reared zoo	-5.217	2.70	-1.931	0.354
Mother-reared zoo - Human	0.847	1.35	0.626	0.987
Unknown - Human	1.174	0.94	1.249	0.792
Wild - Human	-2.116	2.25	-0.941	0.927
Unknown – Mother-reared zoo	0.326	1.25	0.260	1.000
Wild – Mother-reared zoo	-2.963	2.41	-1.227	0.805
Wild - Unknown	-3.289	2.41	-1.468	0.658
P-values corrected for multiple comparisons using Tukey.				

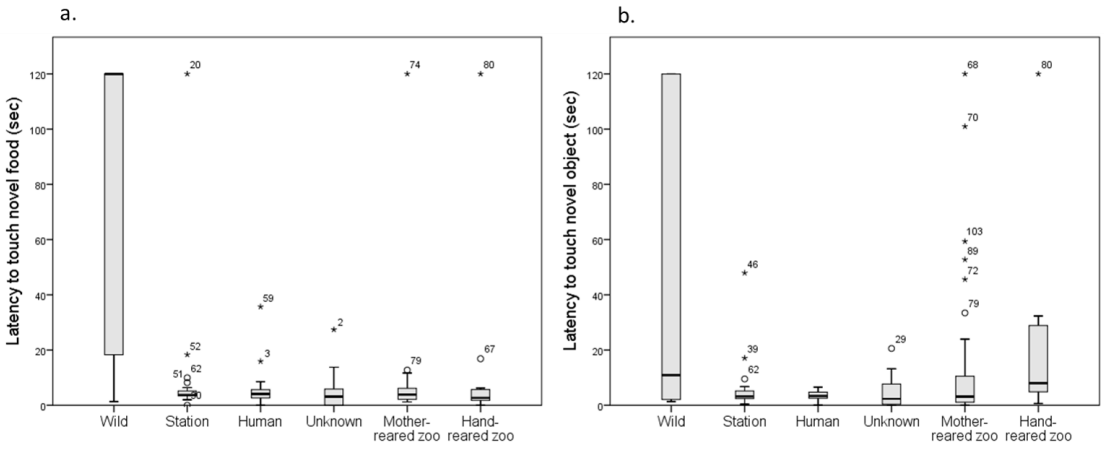

Figure 8: Novelty response across individuals of different background categories. (**a**) Latency to touch novel food and (**b**) Latency to touch a novel object.

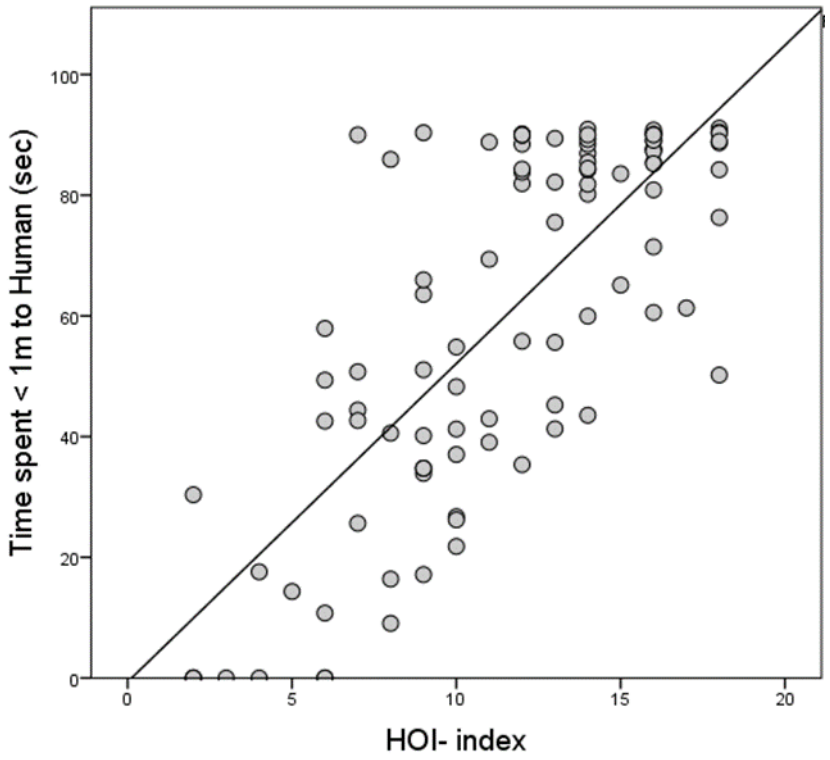

Figure 9: The independent time measurement (seconds a subject spent within one meter to the human stranger) throughout the whole HOI-test strongly correlated with the scored behavioral HOI-index: (Spearman's correlation, two-tailed: r=0.600, N=96, P<0.001).

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2007-2009	*MSc* Evolutionary Anthropology, University of Zurich, Anthropological Institute & Museum. Thesis: *Social Learning and Independent Exploration in immature Sumatran Orangutans, Pongo abelii*
2003-2007	*BSc* Bachelor of Science, Biology, University of Zurich

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2013	*Twycross Zoo*, United Kingdom. Experimental study on orangutan cognition
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2012	A.H. Schultz Foundation, Switzerland: PhD Grant
2013	Georg & Antoinette Claraz Donation: Data Collection Grant
2013	Ella & Georg Ehrnrooth Foundation, Finland: PhD Grant
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External presentations

How human exposure and rearing affect cognitive performance in orangutans. XXVI Congress of the International Primatological Society, IPS Chicago, USA (August 2016)

Testing the Cultural Intelligence Hypothesis on Orangutans: an evolutionary perspective. Behaviour, International Ethological Conference, Cairns, Australia (August 2015)

Determinants of Variation in Orangutans´ Cognitive Performance: Influences of rearing conditions and human exposure. 6th European Federation for Primatology Meeting, EFP Rome, Italy (August 2015)

Why Orangutans? What we can learn from our red cousins. Zonta Award, Jakobstad, Finland (July 2015)

Testing the Cultural Intelligence Hypothesis on Orangutans. European Human Behaviour and Evolution Association, EHBEA, Helsinki, Finland (March 2015)

Testing the Cultural Intelligence Hypothesis on Orangutans. Behaviour & Cognition, Zurich, Switzerland (March 2015)

Testing the Cultural Intelligence Hypothesis on Orangutans: The Effect of Captivity on Orangutan Tool-use. XXV Congress of the International Primatological Society, IPS Hanoi, Vietnam (August 2014)

Orangutan cognition and the captivity effect. Apenheul primate park, Apeldoorn, The Netherlands (February 2014)

Documenting the "Captivity Effect": A change in novelty response between wild and Zoo housed orang-utans.
8th Congress of Gesellschaft für Primatoligie, GfP, Hamburg, Germany (February 2013)

Conservative turns Curious: Response to Novelty and the Captivity Effect in Orangutans.
International Primate Societies Congress, IPS Cancun, Mexico (August 2012)

Social Construction of the Feeding Niche in Orangutans: A Comparative Study
European Federation for Primatology, 3rd International Congress, Anthropological Institute and Museum, University of Zurich, Switzerland (August 2009)

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Forss, S. I. F.; Schuppli, C.; Haiden, D.; Zweifel, N. & van Schaik, C. P. (June 2015) Contrasting responses to novelty by wild and captive orangutans. *American Journal of Primatology.* PDF

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Forss, S. I. F., Damerius, L. A., Kosonen, Z. K., Burkart, J. M., Haun, D. B., Liebal, K., Call, J., Galdikas, B. M., van Schaik, C. P. (Folia Primatologica, August 2015) Determinants of Variation in Orangutans' Cognitive Performance: **II.** Influences of Rearing Conditions and Human Exposure. Abstract

Schuppli, C., **Forss, S. I. F.**, Kunz, J. A., van Noordwijk, M. A., van Schaik, C. P. (Folia Primatologica, August 2015) The Effects of Sociability on Independent Exploration in Wild Immature Orangutans.

Forss, S. I. F., van Noordwijk, M. A., Jaeggi, A. V., Meulman, E. M., van Schaik, C. P. (Folia Primatologica, August 2009) Social Construction of the Feeding Niche in Orang-Utans: A Comparative Study.

Co-authored publication abstracts

The reluctant innovator: orang-utans and the phylogeny of creativity

*Carel van Schaik, Judith Burkart, Laura Damerius, **Sofia Forss**, Kathelijne Koops, Maria van Noordwijk & Caroline Schuppli*

Philosophical Transactions of the Royal Society, February 2016

ABSTRACT

Young orang-utans are highly neophobic, avoid independent exploration, and show a preference for social learning. Accordingly, they acquire virtually all their learned skills through exploration that is socially induced. Adult exploration rates are also low. Comparisons strongly suggest that major innovations, i.e. behaviors that have originally been brought into the population through individual invention, are made where ecological opportunities to do so are propitious. Most populations nonetheless have large innovation repertoires, because innovations, once made, are retained well through social transmission. Wild orang-utans are therefore not innovative. In striking contrast, zoo-living orang-utans actively seek novelty and are highly exploratory and innovative, probably because of positive reinforcement, active encouragement by human role models, increased sociality, and an expectation of safety. The explanation for this contrast most relevant to hominin evolution is that captive apes generally have a highly reduced cognitive load, in particular due to the absence of predation risk, which strongly reduces the costs of exploration. If the orang-utan results generalize to other great apes, this suggests that our ancestors could become more curious once they had achieved near-immunity to predation on the eve of the explosive increase in creativity characterizing the Upper Palaeolithic Revolution.

Observational learning and socially induced practice of routine skills in wild immature orang-utans

*Caroline Schuppli, Ellen Meulman, **Sofia Forss**, Fikty Aprilinayati, Maria van Noordwijk & Carel van Schaik*

Animal Behaviour, September 2016

ABSTRACT

Laboratory experiments have shown that great apes are capable of observational learning and patterns of cultural variation among populations suggest they also use this capacity in the wild. So far, however, the contexts and extent of observational learning in the wild remain unclear. Social learning is expected to be most pronounced during immature skill acquisition. We therefore examined peering (attentive close range watching) by immatures in two populations of wild orangutans (*Pongo spp*.). At total of 1537 peering events, collected during 2571 observation hours were analyzed. We found, first, that peering was most frequent in contexts where learning is expected, namely feeding and nest building. Second, peering in the feeding context was significantly positively correlated with complexity of food processing and with an item's rarity in the mother's diet. Food peering was also followed by significantly increased rates of explorative behaviors with the same food items, showing peering leads to selective practice, and decreased with age and increasing feeding competence of the immatures. Third, the age of peering in the nesting context coincided with the onset of nest-practice behavior, and peering events were directly followed by significantly increased rates of nest-practice behavior. Fourth, the proportion of peering directed at other individuals rather than the mother increased with age. These findings confirm the prediction that immature orangutans learn by observing others through peering. Furthermore, we could show that they do so in a broad variety of contexts. We

conclude that observational learning, followed by socially induced practice, over a period of several years is a critical component of the acquisition of learned subsistence skill acquisition in orangutans.

Development of foraging skills in two orangutan populations: needing to learn or needing to grow?

*Caroline Schuppli, **Sofia Forss**, Ellen Meulman, Nicole Zweifel, Kevin Lee, Maria van Noordwijk & Carel van Schaik*

Frontiers in Zoology, September 2016

ABSTRACT

Background

Orangutans have one of the slowest-paced life histories of all mammals. Whereas life-history theory suggests that the time to reach adulthood is constrained by the time needed to reach adult body size, the needing-to-learn hypothesis instead suggests that it is limited by the time needed to acquire adult-level skills.

To test between these two hypotheses, we compared the development of foraging skills and growth trajectories of immature wild orangutans in two populations: at Tuanan (*Pongo pygmaeus wurmbii*), Borneo, and Suaq Balimbing (*Pongo abelii*), Sumatra. We collected behavioral data on diet repertoire, feeding rates and ranging competence during focal follows, and estimated growth through non-invasive laser photogrammetry.

Results

We found that adult-like diet repertoires are attained around the age of weaning and that female immatures increase their repertoire size faster than their male peers. Adult-level feeding rates of easy techniques are reached just after weaning, but several years later for more difficult techniques, albeit always before adulthood (i.e. age at first reproduction). Independent immatures had faster feeding rates for easy to process items than their mothers, with male immatures achieving faster feeding rates earlier in development relative to females. Sumatran immatures reach adult-level feeding rates 2–3 years later than their Bornean peers, in line with their higher dietary complexity and later weaning. The range-use competence of independently ranging and weaned immatures is similar to that of adult females. Body size measurements showed, immatures grow until female age of first reproduction.

Conclusions

In conclusion, unlike in humans, orangutan foraging skills are in place prior to reproduction. Growth trajectories suggest that energetic constraints, rather than skills, best explain the length of immaturity. However, skill competence for dietary independence is reached later where the adult niche is more complex, which is consistent with the relatively later weaning age with increasing brain size found generally in primates, and apes in particular.

American Journal of Primatology

RESEARCH ARTICLE

Contrasting Responses to Novelty by Wild and Captive Orangutans

SOFIA I. F. FORSS*, CAROLINE SCHUPPLI, DOMINIQUE HAIDEN, NICOLE ZWEIFEL, AND CAREL P. VAN SCHAIK*
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Several studies have suggested that wild primates tend to behave with caution toward novelty, whereas captive primates are thought to be less neophobic, more exploratory, and more innovative. However, few studies have systematically compared captive and wild individuals of the same species to document this "captivity effect" in greater detail. Here we report the responses of both wild and captive orangutans to the same novel items. Novel objects were presented to wild orangutans on multiple platforms placed in the canopy and equipped with motion-triggered video cameras. The same and different novel objects were also presented to orangutans in two different zoos. The results demonstrate extreme conservatism in both Bornean and Sumatran wild orangutans, who gradually approached the novel objects more closely as they became familiar, but avoided contact with them over many encounters spanning several months. Their zoo-living conspecifics, in contrast, showed an immediate neophilic response. Our results thus confirm the "captivity effect." To the various ecological explanations proposed before (reduced risk and increased time and energy balance for captive individuals relative to wild ones), we add the social information hypothesis, which claims that individuals confronted with novel items preferentially rely on social cues whenever possible. This caution toward novelty disappears when human caretakers become additional role models and can also be eroded when all experience with novelty is positive. Am. J. Primatol. © 2015 Wiley Periodicals, Inc.

Key words: novelty response; orangutans; wild; zoo; captivity effect

INTRODUCTION

In recent years, interest in novelty response has soared because it is generally seen as a major source of behavioral innovations and creativity [Auersperg et al., 2011; Greenberg, 1990; Kaufman & Kaufman, 2004; Kaufman et al., 2011; Mettke-Hofmann et al., 2002; Reader, 2003], which in turn are regarded as a good measure of cognitive abilities [Reader & Laland, 2002; Reader et al., 2011]. Novelty response is usually described by two main outcomes, neophilia and neophobia, which are generally considered two independent mechanisms [Carter et al., 2012; Greenberg, 2003; Greenberg & Mettke-Hofmann, 2001; Hughes, 2007; Mettke-Hofmann, 2014; Mettke-Hofmann et al., 2002; Miranda et al., 2013; Pisula et al., 2012; Russell, 1973; Sabbatini et al., 2007]. While neophilia refers to the seeking, approaching, and exploration of novelty, neophobia refers to avoidance of, reluctance to approach, or even fear of, novelty [Greenberg, 1990; Mettke-Hofmann et al., 2006; Mettke-Hofmann, 2014].

The aim of this study was to examine how wild and captive orangutans respond to novel artifacts. As what is novel is highly context dependent, responses may differ both qualitatively and quantitatively [Heyser & Chemero, 2011; Mettke-Hofmann et al., 2006]. Because we could not measure the subjects' internal state [Mettke-Hofmann et al., 2006], and thus could not estimate distress and fear, our focus here is on the observable behaviors. Various other studies have also estimated neophilia/neophobia as approach rates to novel artifacts and/or willingness to feed near them [Benson-Amram et al., 2013;

Contract grant sponsor: Waldemer von Frenckell's Foundation; contract grant sponsor: Paul Schiller Foundation; contract grant sponsor: A. H. Schultz Foundation; contract grant sponsor: Ella and Georg Ehrnrooths Foundation; contract grant sponsor: International Primatological Society

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Received 22 April 2015; revised 18 May 2015; revision accepted 16 June 2015

DOI: 10.1002/ajp.22445
Published online XX Month Year in Wiley Online Library (wileyonlinelibrary.com).

Bergman & Kitchen, 2009; Mettke-Hofmann et al., 2002; Webster & Lefebvre, 2001].

In primates, most studies of novelty response conducted on captive groups describe neophilia [Addessi et al., 2007; Chamove, 1983; Ehrlich, 1970; Glickman & Sroges, 1966; Joubert & Vauclair, 1986; Visalberghi, 1988]. In contrast, the few available studies of wild primates report cautiousness toward novel artifacts [Menzel, 1966; Visalberghi et al., 2003]. To ensure that this difference reflects the contrast between wild and captive conditions, within-species comparisons are required. We know of only two such comparisons with primates. First, after a habituation phase of banana provisioning on platforms, Visalberghi et al. [2003] investigated reactions toward novel food and objects in a group of free-ranging capuchin monkeys, *Cebus apella*. In contrast to captive capuchins [Visalberghi, 1988; Visalberghi & Fragaszy, 1995], wild capuchins consumed very little of the novel food presented to them; furthermore, they delayed approaching both novel food and objects compared to familiar food. A second study, involving rhesus macaques, *Macaca mulatta*, compared captive with semi-free ranging individuals, with similar results [Johnson, 2000]. Thus, in contrast to the curiosity and neophilia reported from captivity, among wild primates novelty seems to elicit avoidance. Among non-primates, the only such comparison involves spotted hyenas, *Crocuta crocuta*, again with the same outcome [Benson-Amram et al., 2013]. Moreover, among primates, there is growing evidence for social influences on the integration of novel food items into feeding repertoires [Addessi et al., 2007; Leca et al., 2007; Schuppli et al., 2012; Ueno & Matsuzawa, 2005; Visalberghi & Addessi, 2000; Visalberghi & Fragaszy, 1995], suggesting that upon encounter with novelty, primates use social cues rather than risk-independent exploration.

Other differences between wild and captive primates in the cognitive domain are consistent with differential responses to novelty, although they may also have other causes. Some primate species are known to use tools only in captivity, and some species using tools in the wild only manufacture them in captivity [Haslam, 2013; van Schaik et al., 1999]. Wild orangutans (*Pongo* spp.), for instance, use a handful of simple tools, such as sticks and leaves, whereas their captive counterparts have a broader tool repertoire, perhaps because human-induced artifacts create a broader range of opportunities than possible with naturally occurring objects [Byrne & Russon, 1998; Russon & Galdikas, 1993; Shumaker et al., 2011]. Moreover, captive baboons, *Papio anubis*, performed better in problem-solving tasks than wild conspecifics [Laidre, 2007], a pattern also confirmed in spotted hyeans [Benson-Amram et al., 2013].

This captivity effect has mostly been explained with reference to environmental factors. Reduced predation and foraging pressure provide captive individuals with a risk-free environment, abundant free time, and excess energy [Benson-Amram et al., 2013; Haslam, 2013; Kummer & Goodall, 1985; Laidre, 2007]. In addition, it has been suggested that the exposure to man-made objects reduces neophobia and enhances object handling [Benson-Amram et al., 2013; Laidre, 2007; van de Waal & Bshary, 2010]. Further, in some species the social environment also differ in captivity not only resulting in increased social contacts with conspecifics [Haslam, 2013], but also social influence on behavior caused by the ability to attend to humans [Fredman & Whiten, 2008; Hirata et al., 2009]. It is therefore worth exploring the role of novelty response in the overall cognitive differences between wild and captive conspecifics.

The purpose of this study was to compare the novelty response between wild and zoo-living orangutans in order to examine to what extent we could replicate the "captivity effect" in novelty reactions within this species. We tested novelty responses in two wild populations, one on Sumatra (*Pongo abelii*) and one on Borneo (*Pongo pygmaeus wurmbii*). We also did two different kinds of zoo controls, one in which the exact same items were used and one in which other novel items were used.

METHODS

The Wild Populations

The experiments on novelty response were conducted on wild orangutans in Indonesia at two study sites: Suaq Balimbing on Sumatra and Tuanan on Borneo. The study site of Suaq Balimbing is situated in the Kluet region of the Gunung Leuser National Park in the province of Nanggroe Aceh Darussalam (03°39′N, 97°25′E). The Tuanan research site is located in the Mawas Reserve in the Central Kalimantan province (2°09′S, 114°26′E). At Suaq, the experiment was conducted between November 2010 and April 2011, and at Tuanan between August 2010 and April 2011. During these periods, 28 orangutans were followed as focal subjects and regularily seen in the study area of Suaq Balimbing; eight adult females, two flanged males, four unflanged males, seven adolescents, and seven infants. At Tuanan, 28 individuals were regular subjects of focal follows; seven adult females, seven flanged males, two unflanged males, five adolescents, and seven infants. The procedures for these experiments were approved by the Department of Forestry and Nature Conservation (PHKA) of the Republic of Indonesia and complied with the American Society of Primatologists' (ASP) Principles for the Ethical Treatment of Primates.

During the time period of these experiments we exposed the orangutans in their natural habitat to

Fig. 1. Platforms and novel objects presented to the wild orangutans: A fresh made orangutan night nest (**a**); a platform nest made to present the novel objects in the forest (**b**); a quadratic red Swiss flag presented together with plastic fruits (**c**, **d**); plastic flowers (**e**), and an orangutan doll (**f**).

items they had never encountered before. The novel materials presented were placed upon natural-looking platforms high in the canopy at various sites in the center of the study area, where the home ranges of many known females overlap. Because wild orangutans are occasionally seen exploring old nests in search of insects or re-building them for their own resting purpose, the platforms were established on a rattan base covered with leaves and branches of familiar tree species woven together to resemble orangutan nests, so the subjects would react toward the novel items rather than the construction itself (Fig. 1a and b).

In Suaq, 15 such platforms were placed at the most common travel height of orangutans within this habitat, 15–30 m [Prasetyo et al., 2009], in four different tree species: *Tetramerista glabra, Horsfieldia polyspherulla, Parastemon urophyllus*, and *Sandoricum beccarianum*. The tree species and exact location for the platforms were selected based on ranging patterns and most visited feeding trees, where the orangutans passed by on a regular basis (Fig. 2). In Tuanan, where the forest canopy is lower, ten platforms were put up on a height of 10–15 m in the following species in the center of the study area (Fig. 2): *Syzygium sp., Notophoebe umbeliflora,*

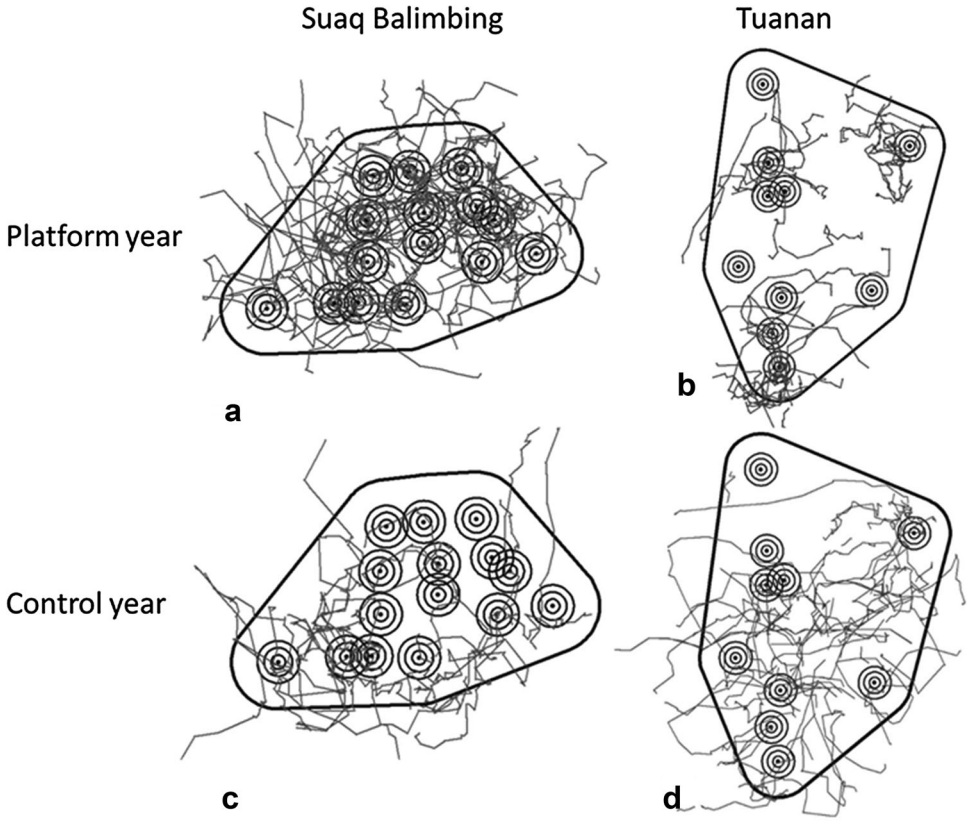

Fig. 2. **a** and **b:** Suaq Balimbing and Tuanan: orangutan travel routes and passes by the platform locations (30 m, 60 m and 90 m) during the experimental time period 2010–2011. **c** and **d:** Suaq Balimbing and Tuanan: travel routes and passes by the platform locations (no platform) during the control period (Suaq Balimbing: 2013–2014, Tuanan: 2012–2013).

Shorea parvistipulata, Dyera lowii, Neoscortechinia kingii, Sandoricum borneense, and *Payena leerii*.

The novel objects presented on the platforms were yellow, white, or pink plastic flowers, a small red quadratic flag (Swiss) in combination with plastic fruits and a small plush orangutan doll (40 cm) (Fig. 1c–f). Plastic flowers were chosen because their colors stood out against the otherwise green canopy but also might be visually recognized from a distance as a potential food item. Orangutans occasionally feed on flowers from multiple different species familiar to them. The red quadratic flag represented a shape–color combination not naturally occurring in orangutan habitats. It was placed above the platform in order to draw attention to the location and the explorable plastic fruits on the platform below it. The orangutan doll could potentially at a distance resemble an infant sitting on a nest, but at closer proximity perceived as a novel stimulus.

During focal follows at both Suaq Balimbing and Tuanan throughout the experimental period, we recorded all approaches toward a platform within 30 m (the approximate distance at which objects can be seen in the mid-canopy) using standardized focal protocols and ad libitum data [Martin & Bateson, 2007]. Focal methods basically followed van Schaik [1999]; a complete description can be found at: www.aim.uzh.ch/Research/orangutannetwork.html. At Suaq Balimbing, we additionally recorded all approaches to <10 m to a platform, gaze direction if at <10 m and any other responses (when present) of the orangutan. In order to maximize data collection but also to control for human influences on novelty response, five of the fifteen platforms at Suaq Balimbing and four out of ten at Tuanan (one camera less due to technical problems) were equipped with small and inconspicuously placed infra-red-motion-detection video cameras (DVREye Pixcontroller, PixController, Inc, Murry Corporate Park, Export, PA). The cameras were installed to record videos both day and night; batteries lasted up to 3 weeks, mainly depending on the number of motion-triggered events. The cameras were situated 2 m in front of the platform to ensure covering all possible physical interactions on or with the platform.

The Captive Populations

It may be difficult to compare wild and captive conspecifics, because zoo-living subjects have been exposed to a wide variety of artifacts, making it harder to decide what is truly novel for them rather than merely similar and thus somewhat novel. We thus use the term "novel" for artifacts never seen before by our subjects and adopted a dual approach. In our first control experiment with a zoo group, we used the same objects that had previously been tested in the wild populations. For the objects used in the wild, we chose natural-looking artifacts in order to reduce the degree of novelty, as captive subjects may have more experience with artifacts in general. In an additional experiment on another zoo group, we presented subjects with two novel items of different categories, albeit different from the ones used in the wild, presented in the open. The data collected with the captive populations complied with the Swiss animal protection law and consisted only of non-invasive experiments and behavioral observations in accordance with the principles of the American Society of Primatologists (ASP).

The first control experiment was conducted on seven Sumatran orangutans, *P. abelii*, housed in the Zurich zoo: one unflanged male, one male infant, and five adult females, one of whom experienced her first pregnancy. The captive subjects were housed in an indoor enclosure of 480 m^3 connected with an outdoor area of 188 m^3. Every morning these orangutans are briefly sent into their sleeping quarters or a smaller room while their enclosure is being cleaned. As the orangutans are let back into their main enclosure, they can encounter enrichment objects such as old footballs, rubber pieces, cardboard boxes, and paper sacks, within which food is occasionally hidden. These are provided routinely and the orangutans are very familiar with the cleaning process and the objects normally lying around in their enclosure. In order to keep everything as normal as possible during the experimental observations, in the morning after enclosure cleaning, the zookeeper placed the novel objects on the floor in the middle of the enclosure. The orangutans would enter their enclosure from different sleeping quarters at slightly different angles to the object location, but the objects were detectable from all different perspectives. We performed the novelty experiments during three continuous days in December 2011, presenting one type of novel object each day.

Based upon information by the keepers, this group of subjects had never encountered any of these or similar artifacts before. However, the red quadratic flag was excluded from the captive part of this study, because these zoo orangutans are provided with red rectangular paper sacks on a regular basis, and a red flag would therefore not represent any particular novel shape or item to them, and also was not needed to draw attention in the open enclosure. The experimental time was set to 1 hr, although in all sessions the experiments were discontinued earlier because the objects had been torn into small pieces. The enclosure was video recorded from two different angles throughout the experimental sessions with two SONY HDV handy cameras (Sony Corporation, Switzerland). Time to first approach until contact with the objects, exploration spans, defined as durations of the manipulations of the objects, and distances to other group members were recorded directly at the test sessions as well as subsequently from the videos. As a control condition we used the video recordings of one morning without any novel objects; the same data were collected on

interactions with objects familiar to the orangutans in this zoo. On this randomly picked day the familiar enrichment items were red paper sacks and cardboard boxes.

The second control experiment involved slightly different novel artifacts. It was conducted in February 2009 on seven Sumatran orangutans, *P. abelii*, housed in Frankfurt zoo. This group of captive subjects was kept in a 253 m^2 enclosure and consisted of one flanged male, three adult females, two immature males, and one immature female. In this data set each subject was tested individually, except for mothers with dependent offspring (the latter would not participate in the test). On any given day, one individual was tested with one novel item in their main sleeping quarter. The following novel artifacts were presented on a small open platform: a soft blue rubber ball (diameter 13.5 cm) normally functioning as a dog toy and an Osram LED light, as a control condition approach latencies towards an empty platform were used. The degree of novelty inevitably differed somewhat between the used artifacts: due to the subjects' previous experience with old footballs, the blue rubber ball might be less novel to them than the flashlight. All experiments were video recorded and analyzed using Mangold INTERACT 8 (Mangold International GmbH, Arnstorf, Germany).

All statistical tests were run in SPSS 19. For the wild population of Suaq we had more detailed data on distances and gaze direction; here we used binary logistic regression to calculate the minimal distance at which gaze directed toward novelty occurred, and thus the platform was noticed by the orangutan. We used Spearman rank correlations to investigate the relationship between approaches to novelty and exposure time. For the zoo population, we used the non-parametric Friedman's test, with additional post hoc analysis [Siegel & Castellan, 1988] in order to correct for multiple comparisons with the same subjects. All the data on the captive study at Zurich zoo was taken by SF and in Frankfurt zoo by DH. The data on the wild populations was taken by SF and NZ, accompanied by well-trained field assistants. All the data used in the analyses from the wild involve distances; these are frequently measured by all field staff in our study and trained with calibrated poles.

RESULTS

Response to Novelty in Wild Orangutans

At Suaq Balimbing, platforms were maintained for 145 days and at Tuanan for 251 days. We first needed to exclude the possibility that there was something about the platform locations, other than the novel objects per se, that kept the orangutans from approaching them. The tree species itself, in which the novel objects were placed, did not influence the likelihood of approaching a platform ($\chi^2(1,6) = 8.316$, $P = 0.216$, $N = 71$). Furthermore, we used ArcGis and GPS data to compare the range use patterns of the focal orangutans in the area with the platforms during the experimental period to a control period (the following year: Suaq Balimbing 2013–2014, Tuanan 2012–2013), when orangutans were followed during the exact same time period (and fruiting season), but in the absence of any platforms or cameras. We calculated the rates at which the orangutans passed the platforms at a distance of <30 m, <60 m, and <90 m during the experimental period (Fig. 2a and b), and repeated exactly the same analysis during the subsequent period, examining the passing of the same locations as where the platforms had been situated (Fig. 2c and d).

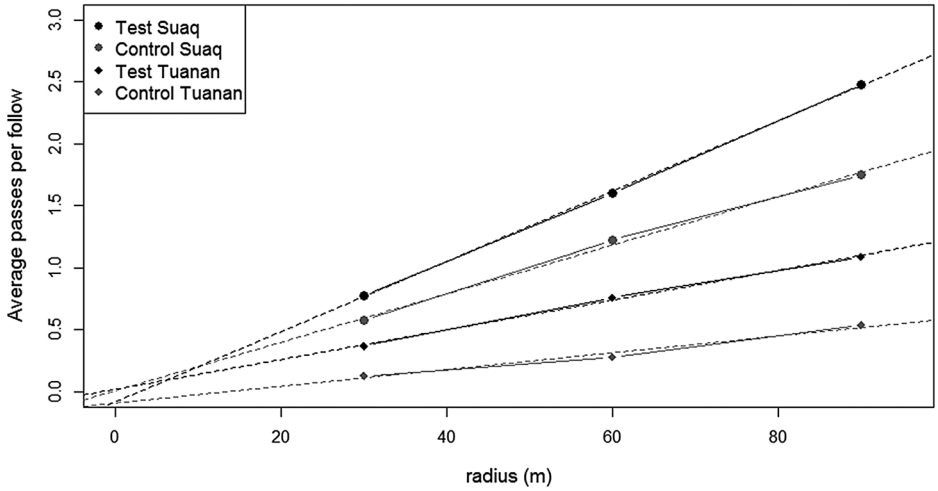

Fig. 3. Average passes per full-day follow by wild orangutans at 30 m, 60 m, and 90 m distance from the platform locations during the experimental year 2010–2011 (test) and during the control periods, when no platforms were present. The straight lines are fitted linear regressions. Note that they all approximately intersect the origin, suggesting no avoidance of the imaginary 30 m circle around the platform.

The average passes per focal follow for both study sites, Suaq Balimbing and Tuanan (test- and control period), are shown in Figure 3. The passing rates of the imaginary circles (30 m, 60 m, and 90 m) of the platforms during the control phase were slightly lower, because we had used the observed traffic patterns right before the experimental period to decide on the locations of the platforms in order to maximize the possible approach rate. However, there was no evidence that the imaginary 30 m circles around platforms were avoided (Fig. 3). We fitted regression lines to the average rate of passes per follow as a function of distance from the platform locations to assess whether movement was basically random. If there was avoidance of the closest circles to the platform, the fitted lines would intersect the abscissa at values well below zero. The regression lines approximately pass through the origin and their confidence limits all include zero, as expected when movement was random relative to platform location. Similarly, the observed 30 m points during the experimental period do not lie clearly below the line connecting the origin and the rates observed at 60 m and 90 m distance. Because the ranging patterns of the orangutans were random relative to the 30 m circle surrounding the platform, we conclude the orangutans showed neither active avoidance of, nor active attraction to the general area around the platforms during the experimental time period.

In the focal follows during the observation period, 59 cases were recorded at Suaq where an orangutan passed the platforms within possible viewing distance (30 m). The number of recorded approaches across the 28 focal followed individuals ranged from 0 to 10. In addition, the motion-triggered video camera traps captured 12 additional independent passes when no human was present (none of which involved physical contact). In total at Suaq 49 approaches to 10 m or closer were noted. At Tuanan, 20 approaches within 30 m were recorded during focal observations, plus none captured on camera (Table I). Because the focal data per individual were too sparse, we used the average pass rate (entering the imaginary 30 m circle) during all focal follows in the experimental period to characterize the average rate for the local population of coming close enough to the novel objects to view them. This rate, as extracted from GPS data in the platform area, was 0.78 per follow for Suaq and 0.37 for Tuanan (Table I). No individuals, apart from two adolescents Shera and Jerry (see below), were recorded to proceed until physical contact with the objects on the platforms during the experimental periods of 145 and 251 days for Suaq and Tuanan.

At Suaq, data was taken on close proximity and gaze direction toward the platforms. At this study site, from 59 recorded approaches to within at least 30 m, 49 were to within 10 m or less. Wild orangutans would direct gaze significantly more toward the platform while they had approached to within 10 m radius than when farther away (binary logistic regression: $N = 59$, Exp (B) = 0.861, $P = 0.006$, Fig. 4). This implies that at a 10 m distance, the orangutans had usually noted the platform. For all focal follows at Suaq Balimbing we calculated the approach rates (corrected for focal time of each individual) and found that as time went by and the novel objects thus became gradually more familiar, individuals were more likely to approach to within 30 m (Spearman's ρ: $r = 0.260$, $N = 48$, $P = 0.081$,

TABLE I. Approaches to the Platform by Wild Orangutans at Suaq Balimbing (Sumatra) and Tuanan (Borneo)

Data recorded in the wild populations	Suaq balimbing	Tuanan
Number of approaches recorded during focal observations	59	20
Number of approaches recorded by video camera trap	12	0
Average passes (<30 m) per follow day	0.78	0.37
Average passes (<60 m) per follow day	1.60	0.76
Average passes (<90 m) per follow day	2.48	1.09
Number of experimental days	145	251
Number of days until first physical interaction with platform	110 (Shera)	74 (Jerry)
Number of focal follows (>6 hr) in the area during experimental time period	139	311

Fig. 4. Median distance to platform, provided the focal animal had approached to within 30 m to the platform, when it did not direct its gaze toward the platform with novel objects ($n = 26$) versus when it clearly did ($n = 33$).

Fig. 5a). Furthermore, we found that the minimum approach distances, provided there was a close approach to 10 m or less, decreased over time (Spearman's ρ: $r = -0.439$, $N = 49$, $P = 0.002$, Fig. 5b). Thus, as time of exposure increased the orangutans gradually approached the objects more closely.

The first and only time a wild orangutan at Suaq made contact with a platform and physically explored its contents was after 110 days. Similarly, at the study site of Tuanan the first and only physical approach was recorded after the novelty had been presented for 74 days (Table I). The adolescent female that explored the novel objects at Suaq Balimbing (Shera) only approached after her attention had inadvertently been drawn to the platform because she noted a human restoring the platform. After observing the person handling the objects on the platform from a distance, the female approached immediately after the human had climbed down. She moved onto the platform and picked up a plastic red apple and tried to bite in it. After several biting attempts she made a tool out of a small twig and poked at the plastic apple with her twig tool. After unsuccessful attempts with the twig tool she picked up a second red plastic apple and tried a third processing technique by striking it back and forth onto a branch. Shera's manipulation involved a feeding technique frequently used in her population, twig tool use [van Schaik et al., 1996]. Further, her exploration span resembles the one measured in captive orangutans handling the same objects for the first time (Fig. 6). Besides this one approach of physical exploration of the novelty, throughout the same time period at Suaq, 28 cases were recorded during focal follows, where an orangutan would explore a normal old nest, but no cases were seen where an orangutan handled the novel objects. The only individual in Tuanan who approached and physically explored the plastic flowers was a male adolescent (Jerry).

Both exploring individuals were adolescents. After their exploration of the novel objects no further physical investigation by the same individuals were recorded within the experimental time period. However, Shera passed a second platform with exactly the same objects on the same day only a few hours after she examined the plastic fruits for the first time. The second time around she approached to zero meters of the platform but only visually examined them and did not touch the plastic fruits presented there.

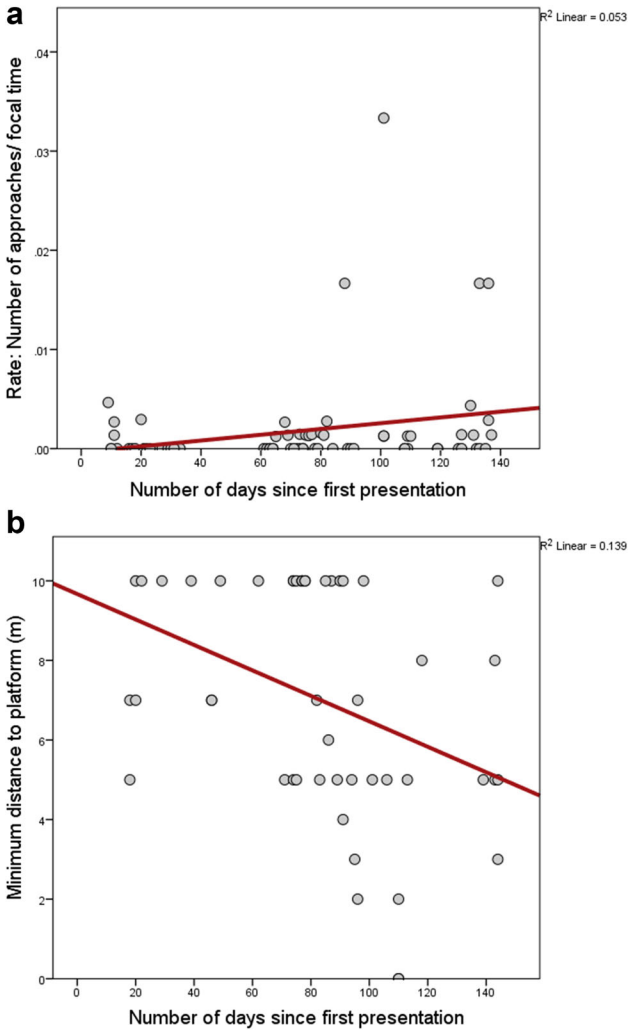

Fig. 5. **a:** Approach rates (number of approaches ≤30 m per hour focal time) for all individuals with at least five approaches recorded during focal follows as a function of the time elapsed since the novel objects were first presented (exposure time); **b**: relationship between all close approaches (≤10 m) and exposure time. The data refer to the wild population of orangutans, *P. abelii* at Suaq Balimbing.

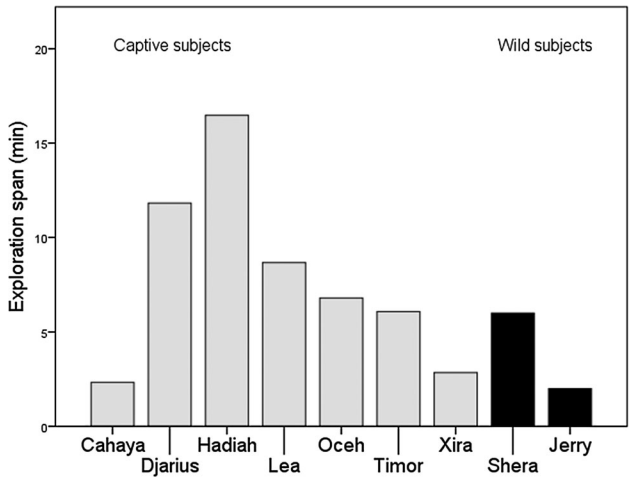

Fig. 6. Comparison of exploration spans (in min) between wild (black bars) and captive (gray bars) subjects handling a novel object: a plastic fruit.

Before these first contacts by the adolescents, it is highly unlikely that an orangutan at either site had approached to such close proximity that examination or manipulation of the novel objects would have taken place. First, in five of the 15 platforms at Suaq and four of 10 at Tuanan, such an event would have been recorded by the video camera, because the cameras did capture a diverse range of other animal species visiting the platforms. Second, not a single object was removed or dropped from the platforms, nor did the objects show any bite marks or other signs of physical exploration or disturbance. By using a crude estimate of approaches (mean number of 30 m passes per follow day times experimental days), by the end of the experiment the average orangutan at Suaq Balimbing had passed the platform location approximately 113 times, or 93 times at Tuanan, without ever handling the objects. However, it has to be noted that this estimate is based on the assumption of equal travel patterns for all individuals.

Neither Shera nor Jerry was unusually keen to approach the platforms: 0.44 per follow day ($N = 16$) and 0.25 per follow day ($N = 8$), respectively, close to the average values for their population. Shera's response was similar to that of the population in general, as she too approached the platform to within 30 m more as time went by (approach rate: Spearman's ρ: $r = 0.636$, $N = 13$, $P = 0.019$) and gradually decreased her approach distance when getting to at least 10 m (Spearman's ρ: $r = -0.824$, $N = 6$, $P = 0.044$). By day 110, when Shera made contact with a platform, we estimate that she had passed by (<30 m) roughly 48 times. The respective estimate for Jerry at day 74 at Tuanan would be 19 passes. Moreover, another adolescent at Suaq (Ellie) was observed within 10 m to a platform 10 times during the study period, but never physically explored the novel objects.

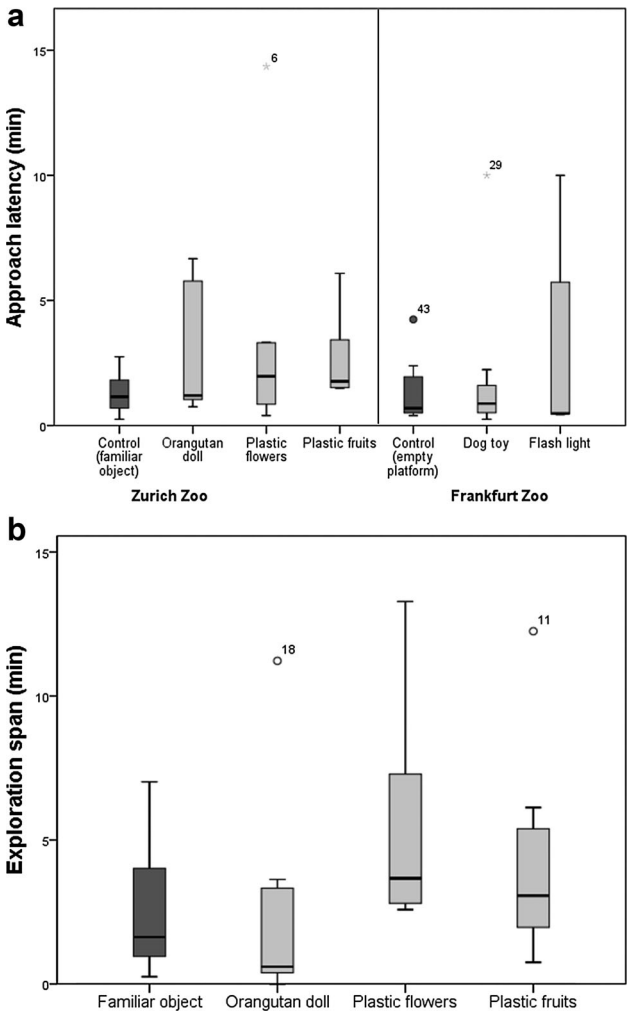

Fig. 7. **a:** Approach to contact latencies (in min) to novel objects by the orangutans in Zurich zoo (the same ones as used for wild orangutans) and in Frankfurt zoo (a blue rubber ball with holes, normally used as a dog toy, and a flashlight), compared with those to familiar objects or an empty platform, respectively, serving as a control condition; **b:** Total exploration time in minutes for the orangutans at Zurich zoo handling a familiar object and three novel objects.

Response to Novelty in Captive Orangutans

In Zurich zoo, the general approach latency towards novel objects was quite different: the Sumatran orangutans approached all novel objects tested within a few minutes (Fig. 7a). They had similar approach latencies for the novel objects as for the familiar objects in the control condition (Friedman's test: χ^2 (3) = 5.229, $N = 7$, $P = 0.156$). Similarly, the Sumatran orangutans housed in Frankfurt zoo approached the presented novel objects equally fast as the control condition when the platform was empty (Friedman's test: χ^2 (2) = 0.519, $N = 7$, $P = 0.772$) (Fig. 7a). In both zoo groups approach latencies varied individually, but were similar between the zoos despite the fact that experiments were performed in the group in Zurich and individually in Frankfurt. In the Zurich group, the wider distribution of approach latencies toward the novel objects versus the control condition, especially the orangutan doll, was probably caused by the fact that only a single doll was presented in their enclosure. Therefore, not all individuals had access to it simultaneously, whereas the familiar objects and the bundles of flowers and fruits could be thorn apart for investigation by multiple individuals. In Zurich, because of the dominance hierarchy (S. Lehner, unpublished data), the two older females could not approach while the doll was being monopolized by the adult male.

In Zurich zoo, where familiar objects served as a control condition, exploration spans were significantly different between conditions (Friedman's test: χ^2 (3) = 8.657, $N = 7$, $P = 0.034$), but using post hoc analyses and applying a Bonferroni correction, pairwise comparisons revealed that none of the durations between the control condition

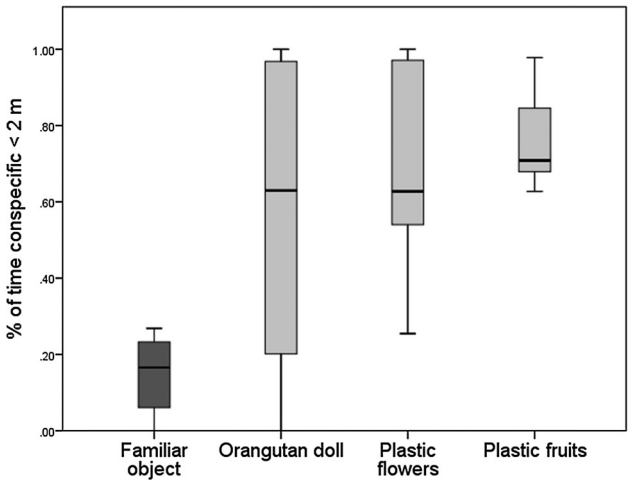

Fig. 8. Comparison of close social proximity (<2 m) when handling a familiar object versus novel objects presented to the orangutans at Zurich zoo.

and the novel objects were significantly different (between all condtions the critical difference at $P = 0.05$, corrected for multiple comparisons, was 12.74, Fig. 7b) [Siegel & Castellan, 1988].

Social proximity during novelty response in Zurich increased during the physical exploration of novel objects. A social partner was significantly more likely to be within two meters when a subject handled one of the novel items than when it was engaging with the familiar paper bags or cardboard boxes (Friedman's test: χ^2 (3) = 9.927, $N = 7$, $P = 0.019$, critical difference = 12.74, Fig. 8). During this closer proximity individuals often tried to grab the novel item from the individual handling it.

DISCUSSION

Wild Versus Zoo Orangutans

Wild orangutans were extremely unresponsive toward the novel artifacts. In fact, the novel objects did not elicit any particular reactions for several months, and therefore we could only report approach data, except for the two cases in which individuals actually handled the novel objects. Although not all platforms were supplemented with cameras, the absence of any physical contact by the orangutans is highly plausible. First, whenever we checked the platforms, the objects showed no signs of having been handled or bitten, and were never found to have been removed. Second, we recorded no contacts during focal follows, except for the two cases of physical interaction (which also left obvious signs of handling on the platforms). Closer approaches were more frequent as time went by (Fig. 5a and b), and these closer passes were accompanied by visual inspection at a distance, suggesting gradual habituation to the novelty but no approach proceeding to physical exploration of the artificial objects. The two adolescents who eventually responded (one in each population) did so after several months of potential exposure. Indeed, contact latencies amounted to dozens of passes in the wild, even for the two adolescents who made contact after an estimated 48 and 19 passes (the latter necessarily are estimates, extrapolated from their mean number of passes per follow day). Although the others orangutans had passed the platforms with novel objects at <30 m about 100 times, they did not make contact with them.

In contrast to their wild counterparts, zoo orangutans approached almost immediately after noticing the novel objects for the first time, regardless of whether they were the same items as used in the wild (Zurich zoo) or other perhaps somewhat more novel objects (Frankfurt zoo), and irrespective of whether they were tested as a group (Zurich) or alone (Frankfurt). Thus, their contact latencies correspond to a single pass in the wild, and contact ensued within a few minutes at most. Zoo orangutans approached all the novel objects as fast as the control conditions of familiar paper sacks and cardboard boxes or an empty platform (Fig. 7a and b).

In the zoo setting the subjects also spent equal time exploring the novel objects as they did the familiar ones (Fig. 7b), suggesting interest in the unfamiliar even though no success in food search followed. Even if the zoo subjects regarded the novel objects as less novel than their wild counterparts, given their previous enrichment experience, they were clearly equally willing to approach and explore the novel objects as the familiar ones. This indicates that these groups of zoo-housed orangutans do not distinguish novel items as irrelevant nor potentially harmful compared to familiar ones.

The comparison, though producing a striking contrast, was not entirely unbiased. First, the animals tested in Zurich zoo were always in association, and it has been shown that association reduces neophobia so that novelty is approached faster in a group context than alone [Marzlufi & Heinrich, 1991; Stöwe et al., 2006]. However, in the study performed at Frankfurt zoo each subject was tested individually and showed similar short approach latencies. Moreover, the orangutans at Suaq are also frequently in association [van Schaik et al., 1999], so differential sociality can only explain a small part of the difference. Second, novelty may cause stronger reactions in a familiar environment [Harris & Knowlton, 2001], and the zoo animals live in far smaller enclosures than their wild counterparts. However, the latter are obviously also very familiar with their habitat, [e.g., Janmaat et al., 2012], and continued to show no response toward the novel objects after dozens of passes. Thus, while the comparison cannot be made totally unbiased, the dramatic difference we observed is real and requires explanation.

Explaining the Captivity Effect

This documented marked difference between wild and zoo orangutans in their response to artificial novel objects suggests that something about these two conditions fundamentally changes the response to novelty. So far, the main explanation has referred to time constraints. Due to the lack of predation pressure and foraging challenges, captivity has been argued to provide animals with a more relaxed time budget [Kummer & Goodall, 1985] or an excess of energy [Benson-Amram et al., 2013], allowing for more exploration. However, Benson-Amram et al. [2013] demonstrated that the higher problem-solving ability in captive versus wild spotted hyenas could be attributed to reduced neophobia rather than differences in time and energy. Thus, while the reduced attentional and perceptual load in captivity (due to lack of predation or the need to search for food and plan the daily routes) may free up animals to become more exploratory, having more free time per se does not explain reduced neophobia.

One key factor may well be risk [Haslam, 2013; Kummer & Goodall, 1985]. Wild orangutans cannot know whether novel objects are dangerous, and given their long life expectancy [Wich et al., 2004] may benefit from being conservative. Because exploration times themselves were similar for zoo and wild orangutans, once the latter approached the items (Fig. 7a and b), the difference between the wild and captivity is truly in the lack of avoidance of novelty. Risk assessment surely differed between the two conditions. Zoo-living animals only have positive experiences with novel items, which are usually food or playthings, and thus may have overcome any initial neophobia as a consequence of positive reinforcement with man-made objects. In fact given the less diverse environment of a zoo, the zoo subjects may have seen the artifacts as worth approaching and exploring. Their wild counterparts clearly did not. This may appear surprising, given that in the wild especially immature orangutans can spend up to 45% of their daily activity budget engaged in play, including play with familiar objects in their habitat [van Noordwijk et al., 2009]. On the other hand, exploration spans were similar between wild and captive subjects once an approach was made. If limited time and energy determined the response, this would not be expected.

While lack of risk and increased value of the objects may cause part of the documented difference between wild and captive orangutans in our study, we also propose social information as a complementary explanation. One obvious way to avoid risk when dealing with novelty is to use social information. Naive wild orangutans can attend to role models and heavily rely on social learning in the acquisition of their diet. Maturing individuals with abundant opportunities for social learning have come to rely preferentially on socially learned skills to construct their cognitive abilities [the cultural intelligence hypothesis: van Schaik & Burkart, 2011; see also Herrmann et al., 2007; Whiten & van Schaik, 2007]. They thus follow experienced role models around and minimize independent exploration [e.g., orangutans: Jaeggi et al., 2008; Jaeggi et al., 2010; van Schaik et al., 2003]. As a result, naive orangutans tend not to interact with novel features in their environment until they have seen experienced role models interact with them. Rare food items are more likely to be unfamiliar to these naive immatures, and indeed in their natural environment, orangutan infants focus much more visual attention toward their mothers when the latter are feeding on food items that are very rare in the feeding repertoire [Jaeggi et al., 2010; C.S., unpublished]. Interestingly, unfamiliar objects in captivity also elicited social attention (Fig. 8). Thus, the availability of social information is consistent with the novelty avoidance in wild orangutans.

This account suggests that novelty avoidance is the natural response of wild orangutans. The availability of social information can help us understand the loss of novelty avoidance in captivity because in a zoo environment, human keepers serve as additional role models. Once these conditions are in place, the greater opportunity for social learning due to intense contact with conspecifics maintains and even boosts this captivity effect. Thus, we suggest that in species that have the ability to attend to humans as an additional source of information the neophilia seen in captivity arises in part because the novel items (objects, stimuli, and even spaces to some extent) are associated with humans and thus are implicitly approved for exploration. Indeed, semi-free ranging rhesus macaques have been reported to accept novel food faster when handed to them by humans than when they independently discovered it in their habitat [Johnson, 2000]. Likewise, orangutan orphans reared in rehabilitation centers and sanctuaries, experience human role models as replacement for their own mothers, and when in semi-natural conditions become very exploratory [Russon et al., 2009; Russon et al., 2010].

The two cases of contact in the wild are also consistent with a role for social information. When Shera, at Suaq Balimbing, approached and explored the novel objects, her attention had been drawn to them by a familiar human engaging with the objects (note that no physical approach was recorded in the absence of humans by the video camera traps). Furthermore, experiments have shown that infant orangutans refuse novel foods offered by unfamiliar humans unless they witness them being accepted by conspecific adults [Rijksen, 1978]. In general, the presence of conspecifics influence the acceptance of novel food in orangutans [Gustafsson et al., 2014; Hardus, 2012] a pattern also found in some other primate species, e.g.,

aye-ayes, *Daubentonia* [Krakauer, 2004] and capuchin monkeys, *C. apella* [Visalberghi & Addessi, 2000].

Future work should examine the range of species in which the captivity effect can be documented, and moreover what aspects of a captive environment causes novelty response and other behaviors to differ from that in natural habitats. The social information hypothesis predicts that in species with strong orientation toward tolerant role models in regular skill acquisition during development, but also gregarious, tolerant foraging per se, social attendance boosts interest in novelty. However, we stress that this idea is not meant as an alternative to the effects of ecological factors such as limited environmental stimulation, abundant free time and good physical condition. Regardless of the factors causing the captivity effect, an important unresolved question remains to what extent the documented cognitive differences between wild and captive populations [e.g., Laidre, 2007; Benson-Amram et al., 2013] can be attributed to different attitudes towards novelty.

Neophilia and Cognition

Innovations have been shown to correlate with neophilia [Day et al., 2003; Webster & Lefebvre, 2001]. Wild orangutans avoid novelty. Yet, they have large innovation repertoires [van Schaik et al., 2006], and the Sumatran population at Suaq is the technologically most advanced orangutan population, showing a variety of tool uses, which are known to be based on innovations [van Schaik, 2004; van Schaik & Knott, 2001; van Schaik et al., 1996]. Admittedly, the one individual (Shera) at Suaq exploring a plastic apple used a stick tool to do so, but most others at Suaq ignored these novel objects, also after long exposure time. Moreover, we found no major differences between the Bornean and Sumatran sites with regard to reactions after passing within 30 m of a platform.

This comparison thus supports the idea that novelty response and high innovative ability do not necessarily go together [Brosnan & Hopper, 2014; Griffin & Guez, 2014]. First, as noted above, the attitude toward novelty and the tendency to explore are probably independently regulated at the proximate level. There were no differences between the wild and zoo individuals in exploration time, once the latter had proceeded to physical contact with the novel objects. Second, as suggested by the orangutan comparison, highly technologically innovative species, such as great apes, may well owe their large innovation repertoires to their efficient social learning, which strongly increases the chances of persistence of any innovations that happen to have been made [Koops et al., 2014; van Schaik et al., 2003].

ACKNOWLEDGMENTS

We thank the following foundations for supporting grants: the Waldemer von Frenckell's foundation, the Paul Schiller foundation, A. H. Schultz foundation, Ella and Georg Ehrnrooths foundation and the International Primatological Society. We especially thank two anonymous reviewers for the constructive and valuable comments. We also gratefully acknowledge the following Indonesian institutions for their collaboration and work permissions: the State Ministry of Research and Technology (RISTEK), Universitas Nasional (UNAS), especially Drs. Tatang Mitra Setia and Sri Suci Utami Atmoko, the Sumatran Orangutan Conservation Programme (SOCP), in particular Dr. Ian Singleton and Santi Delavita Lubis, Yayasan Leuser Ekosistem (YLI), Taman Nasional Gunung Leuser (TNGL), Badan Pengelolaan Kawasan Ekosistem Leuser (BPKEL), MAWAS, and the Bornean Orangutan Survival Center in Kalimantan, Direktorat Fasilitasi Organisasi Politik dan Kemasyarakatan, Departamen Dalam Negri, The Department of Forestry and Nature Conservation (PHKA), and the Indonesian Institute of Science (LIPI). We also thank Robert Zingg and the Zurich and Frankfurt Zoo for the effective collaboration.

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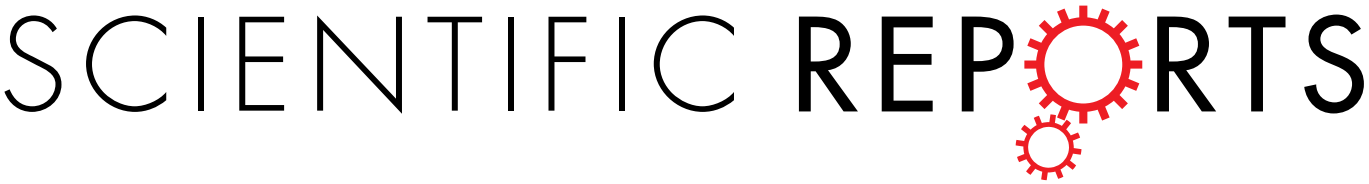

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Cognitive differences between orang-utan species: a test of the cultural intelligence hypothesis

Received: 21 April 2016
Accepted: 06 July 2016
Published: 28 July 2016

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Cultural species can - or even prefer to - learn their skills from conspecifics. According to the cultural intelligence hypothesis, selection on underlying mechanisms not only improves this social learning ability but also the asocial (individual) learning ability. Thus, species with systematically richer opportunities to socially acquire knowledge and skills should over time evolve to become more intelligent. We experimentally compared the problem-solving ability of Sumatran orang-utans (*Pongo abelii*), which are sociable in the wild, with that of the closely related, but more solitary Bornean orang-utans (*P. pygmaeus*), under the homogeneous environmental conditions provided by zoos. Our results revealed that Sumatrans showed superior innate problem-solving skills to Borneans, and also showed greater inhibition and a more cautious and less rough exploration style. This pattern is consistent with the cultural intelligence hypothesis, which predicts that the more sociable of two sister species experienced stronger selection on cognitive mechanisms underlying learning.

Socially mediated learning[1] has been studied mainly because it is increasingly shown to be responsible for geographically distinct traditions in many non-human animals[2–7]. However, social learning also turns out to be instrumental in the acquisition of critical ecological[8–10] and social skills[11,12]. The *cultural intelligence hypothesis* proposes that opportunities to learn skills socially during development facilitate the construction of an individual's intellectual abilities[13,14]. Thus, the greater the quantity and quality of such social inputs during ontogeny, the more learned skills an individual can acquire, but also the more experience it can accumulate and thus the better it will be at asocial learning or problem-solving. This process also generates a larger skill pool in a population, which in turn enlarges the individual's set of learned skills[14].

So far this developmental dimension of cultural intelligence is well supported both in humans[15] and nonhuman primates[16,17]. However, the hypothesis also has an evolutionary dimension, which posits that species with a social system that predictably exposes maturing individuals to numerous opportunities for social learning will be subject to selection on cognitive abilities, whenever fitness is improved by having a larger set of skills, more complex skills, or mastering them earlier in life. Because maturing individuals in such species will routinely accumulate greater experience, they should be more likely to transfer knowledge to other tasks, and thus further improve their ability to solve problems. This process may select for enhanced exploration strategies. Moreover, on longer time scales, such species should also experience selection to enhance the underlying social learning mechanisms. Importantly, due to the cognitive overlap with asocial learning mechanisms[18–20], this selection will indirectly also produce improved asocial learning ability, which over time, will lead to an increase in the innate general cognitive performance in conditions identical to the ancestral state, as well as increased brain size.

The cultural intelligence hypothesis should apply to any species that learns socially and transmits this knowledge across generations, although the strength of the effect is likely to depend on the social learning mechanisms, the number of experts, the duration of the learning period, and the role played by experts. The cultural intelligence found in humans can be regarded as an example of this, because the capacity of infants to attend to skills actively demonstrated by experts is an essential ingredient enabling exchange of knowledge across our cooperative and social lifestyle[15,21]. Thus, humans have evolved unique predispositions in both infants and caretakers towards active skill transmission (pedagogy: see ref. 22). However, apart from the human case, there are very few formal comparative tests of the correlation between social learning and innovativeness[23] or brain size as a proxy for asocial learning or innovation ability[24].

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	B	SE	z value	*P*
Intercept	1.998	1.44		
Species				
Pongo pygmaeus	–	–	–	–
Pongo abelii	1.934	0.74	2.63	0.0085
Confounding variables:				
Task				
Detour reaching	–	–	–	–
HT: Straight trap	−1.446	0.97	−1.49	0.1355
HT: Re-use	−4.147	1.06	−3.92	0.0001
HT: Rope tool	−5.258	1.15	−4.58	0.0000
HT: Curved trap	−6.268	1.27	−4.93	0.0000
Reversal learning	−3.441	1.06	−3.26	0.0011
Tube trap: >60%	−4.260	1.12	−3.81	0.0001
Sex				
Female	–	–	–	–
Male	0.448	0.72	0.63	0.5321
Age	0.006	0.03	0.21	0.8306
Number of Zoos	−0.543	0.31	−1.77	0.0774
Group size	0.122	0.12	0.99	0.3235

Table 1. Output from the generalized linear mixed model (GLMM) showing species differences in task performance. 196 observations on 33 individuals from 9 different zoos, $\chi^2_{ML} = 86.45$, $P < 0.0001$.

Here we tested the prediction that greater opportunities for social learning are associated with a different exploration style and greater asocial learning ability[14]. A systematic comparison of the cognitive abilities of the two orang-utan species (*Pongo abelii* on Sumatra, and *P. pygmaeus* on Borneo, with an evolutionary divergence estimated from autosomal gene pools of around ~0.9–1.1 Ma[25]) provides an excellent test of this prediction. Orang-utans show extensive social learning during skill development[10,26,27], with more frequent peering and subsequent practice as the complexity of foraging skills increases[28]. They also show extensive evidence for geographic variation in a variety of skills[6,29,30]. Crucially, Sumatran and Bornean orang-utans differ systematically in the frequency of the opportunities for social learning. In similar habitats, Sumatran populations show higher densities[31,32] and are consistently more gregarious and socially tolerant[32,33]. They also show much greater repertoires of learned skills and exploratory behaviour[28], along with greater cultural repertoires in general[6]. This difference in socio-ecology has likely persisted over evolutionary time[25,34]. Note that our choice of species provides a particularly stringent test of the hypothesis because their broadly similar brain size[35] means that we test the genetic impact of cultural intelligence before pronounced brain size differences have evolved.

Because housing and rearing conditions, which may range from deprivation to enculturation, have a major impact on the cognitive development of apes[36,37], a proper test of the possibly subtle differences in cognitive performance crucially requires that the conditions be as identical as possible. Since this cannot possibly be achieved in the natural environment, we therefore turned to zoo-housed orang-utans. All subjects in this study were zoo-born and mother-reared, and experienced highly similar feeding routines, sleeping quarters, encounters with human keepers and visitors, out-door enclosures and enrichment regimes. In all, 33 subjects in 9 different European zoos were tested on their physical cognitive skills on 4–7 different tasks inspired by the test battery employed by Herrmann *et al.*[21].

When groups of animals differ in cognitive performance, it is informative to look for underlying differences in their problem-solving strategies, because selection on cognitive performance may actually have targeted these mechanisms. We therefore also tested for the possible role of novelty response, exploration style and inhibitory control, since recent literature has identified these as potentially important mechanisms in conspecific comparisons. First, since cognitive tests inevitably involve some element of novelty, how animals respond to novelty may affect their cognitive performance, as found in several studies[23,38,39]. Second, exploration styles have been reported to influence cognitive performance. Sometimes, the best problem solvers are the boldest individuals[40], at other times, they are the individuals showing frequent and persistent exploration[41,42], whereas in yet other cases, they are those with the most diverse exploratory actions[43]. Finally, some studies suggest a relationship between inhibitory control and higher cognitive abilities[44,45].

Results

We presented orang-utans of the two species with a set of physical-cognition tasks and additionally two tests of novelty response (a novel food and a novel toy).

Cognitive performance. Overall performance, across 7 tasks on physical cognition, was assessed for a total of 33 subjects (14 Bornean, 19 Sumatran) from 9 different zoos (Supplementary Table S1 & Table S2). A highly significant binomial GLMM ($\chi^2_{ML} = 33.24$, $N_{obs} = 196$, $P < 0.0005$; Table 1) revealed that, while controlling for the potentially confounding effects of age, sex, group size, the number of zoos a subject had lived in, and task

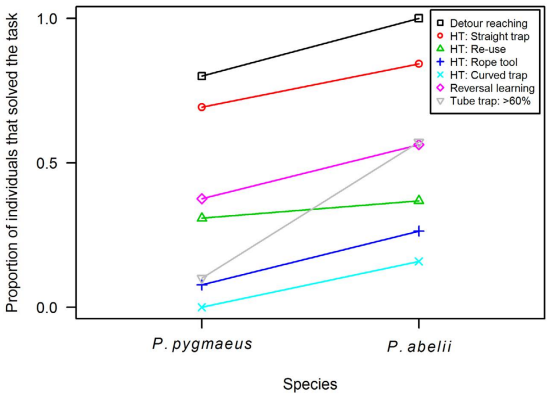

Figure 1. Overall task performance over the different tasks and subtasks by *Pongo pygmaeus* and *Pongo abelii*. Subjects of *P.abelii* were significantly more likely to solve a task than *P. pygmaeus* subjects (Binomial GLMM: $B = 1.934$, $SE = 0.74$, $z = 2.63$, $P < 0.01$).

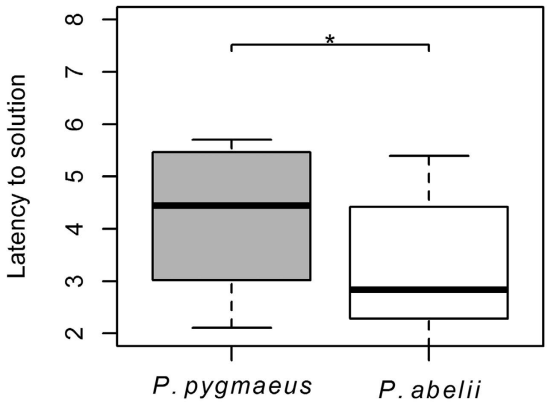

Figure 2. Latency to solution in detour reaching task. Among the subjects who solved the task, Sumatrans showed faster latencies until solution in detour reaching task (LM: $N_{Sumatra} = 10$, $N_{Borneo} = 10$, $P_{species} = 0.049$, $\beta_{species} = -94.53 \pm 44.28$, $P_{age} = 0.155$, $P_{sex} = 0.760$).

identity, Sumatran subjects were significantly more likely to solve a task than their Bornean congeners ($B = 1.934$, $SE = 0.74$, $z = 2.63$, $P < 0.01$, Fig. 1, Table 1). In fact, the odds ratio indicated that the overall odds of a Sumatran subject solving a task were more than 6 times as high as those of a Bornean subject. Our model also reflected that, compared to the detour-reaching task, performance was significantly worse on most other tasks (Table 1). Follow-up models constructed to investigate the interaction between species and task, failed to converge due to singularities in the Hessian matrix. However, visual inspection of a plot depicting the proportion of subjects within each species that solved each task (Fig. 1), suggests that the difference between Sumatran and Bornean individuals was both consistent and of a similar magnitude across all tasks (although possibly more pronounced for the tube trap experiment).

The differences between Sumatran and Bornean subjects actually held across individual tasks and subtasks, even though they were not always significant and we could not control for all the confounding variables in these comparisons. The detour-reaching task measured inhibitory control as well as exploration actions (see methods). Data on latency to solution and exploration behaviour was log transformed in order to reach normally distributed residuals. Our results showed that among successful solvers, Sumatran subjects were significantly faster in solving this problem (LM: $N_{Sumatra} = 10$, $N_{Borneo} = 10$, $P_{species} = 0.049$, $\beta_{species} = -94.53 \pm 44.28$, $P_{age} = 0.155$, $P_{sex} = 0.760$; Fig. 2).

In the honey tool-task consisting of multiple cognitive measurements (see methods), Sumatrans were somewhat more likely to solve the stick solution, but the difference in latencies was not significant (LM: $N_{Sumatra} = 19$, $N_{Borneo} = 13$, $P_{species} = 0.159$, $P_{age} = 0.143$, $P_{sex} = 0.826$). The three individuals who managed to solve the more difficult task of using the rope for the curved trap were all Sumatran.

Because the tube trap task (see methods, Supplementary Fig. S1), was designed with equally many tubes providing the correct solution toward the left and the right side, a subject with a strong preference for one side would correctly solve the problem 50 percent of the time. Thus to reach a higher level in this task an individual had to suppress any existing side preference and instead decide in each instant towards which side to move the food item. We therefore first looked for the existence of a side preference and found that Sumatrans and Borneans

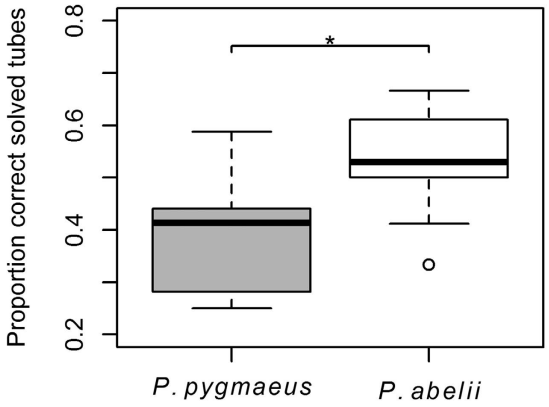

Figure 3. Proportion correctly solved tubes in tube trap task. Sumatran individuals achieved significantly more correct tubes than Borneans (LM: $N_{Sumatra} = 14$, $N_{Borneo} = 8$, $P_{species} = 0.011$, $\beta_{species} = 0.127 \pm 0.045$, $P_{age} = 0.123$, $P_{sex} = 0.737$).

did not differ significantly in the tendency to have a side preference: 70% for Borneans and 85.7% for Sumatrans (Chi-square test: $N_{Sumatra} = 14$, $N_{Borneo} = 10$, $\chi^2 = 2.33$, $P = 0.311$). When comparing the proportion of tubes solved correctly, we found that Sumatran individuals achieved a significantly higher proportion of correct tubes than Borneans (LM: $N_{Sumatra} = 14$, $N_{Borneo} = 8$, $P_{species} = 0.011$, $\beta_{species} = 0.127 \pm 0.045$, $P_{age} = 0.123$, $P_{sex} = 0.737$; Fig. 3).

In the reversal-learning task all individuals in our sample, both Bornean and Sumatran learnt the first association between lid colour and food reward. Further, 37.5% of the Bornean subjects and 56.3% of Sumatran learnt the reverse colour association (Chi-square test: $N_{Sumatra} = 16$, $N_{Borneo} = 8$, $\chi^2 = 0.230$, $P = 0.891$), which did not amount to a significant difference.

Task exploration. We also examined possible mechanisms that could underlie the species difference in cognitive performance, focusing on the latency to ingest novel food, the exploration during tasks as well as of a novel toy, and an assessment of inhibitory control.

Novel food reactions. We compared the two species in their response towards novel food, using their reactions to a familiar food item as the control condition. Data of the response variable (latency to taste novel food) was log transferred in order to reach evenly distributed residuals. We found that the Sumatran species took significantly longer before ingesting the new food than Bornean. Moreover, we found an age effect showing that younger Sumatran subjects would take longer to taste novel food than older individuals. However, this age effect was not found in the Bornean sample: (LM: $N_{Sumatra} = 19$, $N_{Borneo} = 12$, $P_{species} < 0.001$, $\beta_{species} = 2.179 \pm 0.433$, $P_{sex} = 0.726$, $P_{age} = 0.686$, $P_{interaction:\ age/species} = 0.001$, $\beta_{interaction:\ age/species} = -0.071 \pm 0.018$; Fig. 4a,b). Relative to the Bornean sample, our Sumatran sample contained more young individuals who responded with longer delays to try the novel food. To exclude the fact that those young individuals drove the results of novel food reaction, we also ran the same model excluding all individuals younger than six years. We still obtained the same species difference (LM: $N_{Sumatra} = 14$, $N_{Borneo} = 12$, $P_{species} < 0.001$, $\beta_{species} = 2.123 \pm 0.496$, $P_{sex} = 0.990$, $P_{age} = 0.781$, $P_{interaction:\ age/species} = 0.001$, $\beta_{interaction:\ age/species} = -0.069 \pm 0.020$). In the familiar food condition, we found neither a species nor an age effect (LM: $N_{Sumatra} = 15$, $N_{Borneo} = 9$, $P_{species} = 0.340$, $P_{sex} = 0.500$, $P_{age} = 0.257$; Fig. 4c,d).

Exploration styles. We also found species differences in the exploration of a novel toy. Compared with Sumatran-, Bornean orang-utans showed a higher rate of gentle exploration, measured as touching, rotating or sliding the tennis balls presented as the novel toy (LM: $N_{Sumatra} = 19$, $N_{Borneo} = 9$, $P_{species} = 0.031$, $\beta_{species} = -0.163 \pm 0.071$, $P_{age} = 0.069$, $P_{sex} = 0.169$; Fig. 5a) but especially a higher rate of rough exploration, which included hitting, biting or pushing the objects (LM: $N_{Sumatra} = 19$, $N_{Borneo} = 9$, $P_{species} < 0.001$, $\beta_{species} = -0.167 \pm 0.036$, $P_{age} = 0.636$, $P_{sex} = 0.155$; Fig. 5b).

The same species difference in explorative behaviour found in the novel toy test also appeared in the detour-reaching task. Bornean subjects showed significantly more rough exploration (controlled for time at apparatus) than Sumatrans (LM: $N_{Sumatra} = 10$, $N_{Borneo} = 10$, $P_{species} = 0.042$, $\beta_{species} = -0.050 \pm 0.023$, $P_{age} = 0.301$, $P_{sex} = 0.134$; Fig. 5d). We did not find the same effect when comparing gentle exploration (LM: $N_{Sumatra} = 10$, $N_{Borneo} = 10$, $P_{species} = 0.648$, $P_{age} = 0.794$, $P_{sex} = 0.478$; Fig. 5c).

In the honey tool-task, each subject was given ten minutes to engage with the apparatus in order to extract honey using the correct tool for two different traps; straight and curved trap. There was no species difference in either the attentive time (LM: $N_{Sumatra} = 19$, $N_{Borneo} = 13$, $P_{species} = 0.903$, $P_{age} = 0.064$, $P_{sex} = 0.811$, Supplementary Fig. S2a), or the duration of exploration in this task (LM: $N_{Sumatra} = 19$, $N_{Borneo} = 13$, $P_{species} = 0.398$, $P_{age} = 0.094$, $P_{sex} = 0.449$, Supplementary Fig. S2b), indicating that individuals of both species were equally motivated to engage with the task. They also did not differ in the variety of exploration actions (LM: $N_{Sumatra} = 19$, $N_{Borneo} = 13$, $P_{species} = 0.930$, $P_{age} = 0.465$, $P_{sex} = 0.523$, Supplementary Fig. S2c). However, we found that Sumatrans clearly tended to spend more time exploring the relevant parts of the problem-solving apparatus compared to Borneans,

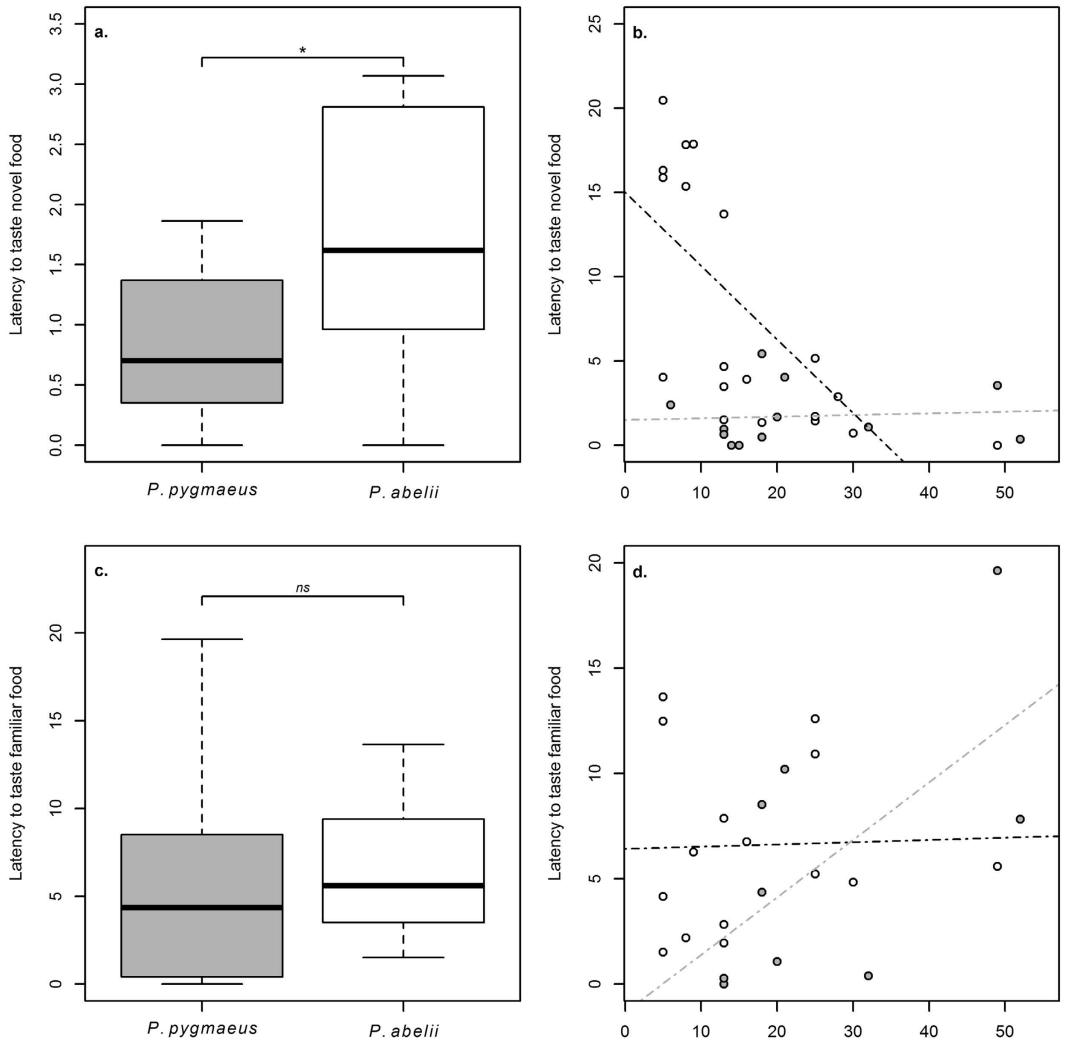

Figure 4. Latencies to taste novel (**a**,**b**) and familiar food (**c**,**d**). Sumatran subjects took longer to taste novel food than Bornean subjects and an interaction effect of age and species was found within the Sumatran subjects: (LM: $N_{Sumatra} = 14$, $N_{Borneo} = 12$, $P_{species} < 0.001$, $\beta_{species} = 2.123 \pm 0.496$, $P_{sex} = 0.990$, $P_{age} = 0.781$, $P_{interaction:\ age/species} = 0.001$, $\beta_{interaction:\ age/species} = -0.069 \pm 0.020$). The familiar food condition showed neither a species nor an age effect (LM: $N_{Sumatra} = 15$, $N_{Borneo} = 9$, $P_{species} = 0.340$, $P_{sex} = 0.500$, $P_{age} = 0.257$).

and that males spent less time on relevant exploration than females (LM: $N_{Sumatra} = 19$, $N_{Borneo} = 13$, $P_{species} = 0.064$, $\beta_{species} = 0.139 \pm 0.072$, $P_{age} = 0.210$, $P_{sex} = 0.029$, $\beta_{sex} = -0.183 \pm 0.080$; Fig. 6).

Inhibition. The reversal-learning task provides the opportunity to examine inhibition. When an individual opens the correct lids it acquires information about the specific colour and presence of a food reward; equally, opening the wrong lids produces information about the absence of a food reward associated with that colour. Once the individual has learned where the food is hidden it should therefore inhibit the tendency to open the wrong lids. We calculated the total number of lids each subject touched and the proportion of which were of the wrong colour and log transferred our data to produce evenly distributed residuals. We found a significant difference between the species: Bornean orang-utans opened more of the wrong coloured lids than did Sumatran, (LM: $N_{Sumatra} = 16$, $N_{Borneo} = 8$, $P_{species} = 0.011$, $\beta_{species} = -0.092 \pm 0.033$, $P_{age} = 0.899$, $P_{sex} = 0.475$; Fig. 7).

Discussion

The results showed a clear and consistent pattern: Sumatran orang-utans, *Pongo abelii,* performed better in a variety of tests of physical cognition compared to the Bornean species, *Pongo pygmaeus* (Fig. 1 and Table 1). In fact, there was not a single task in which Bornean subjects were more likely to solve the problem than the Sumatrans. The results of the GLMM reveal that variation in cognitive performance was strongly determined by species and revealed no significant effect of group size, age, sex, or the identity of the zoo in which they were kept. Moreover, in the detour-reaching task Sumatran orang-utans were faster at achieving the solution, which required inhibition of fixation on the visible food reward (Fig. 2). In the tube-trap task no subject manage to solve more than 12 tubes out of 18, perhaps because most individuals had a side preference, which would have to be suppressed in order to reach a high task performance. Nonetheless, Sumatran orang-utans managed to solve more tubes correctly than

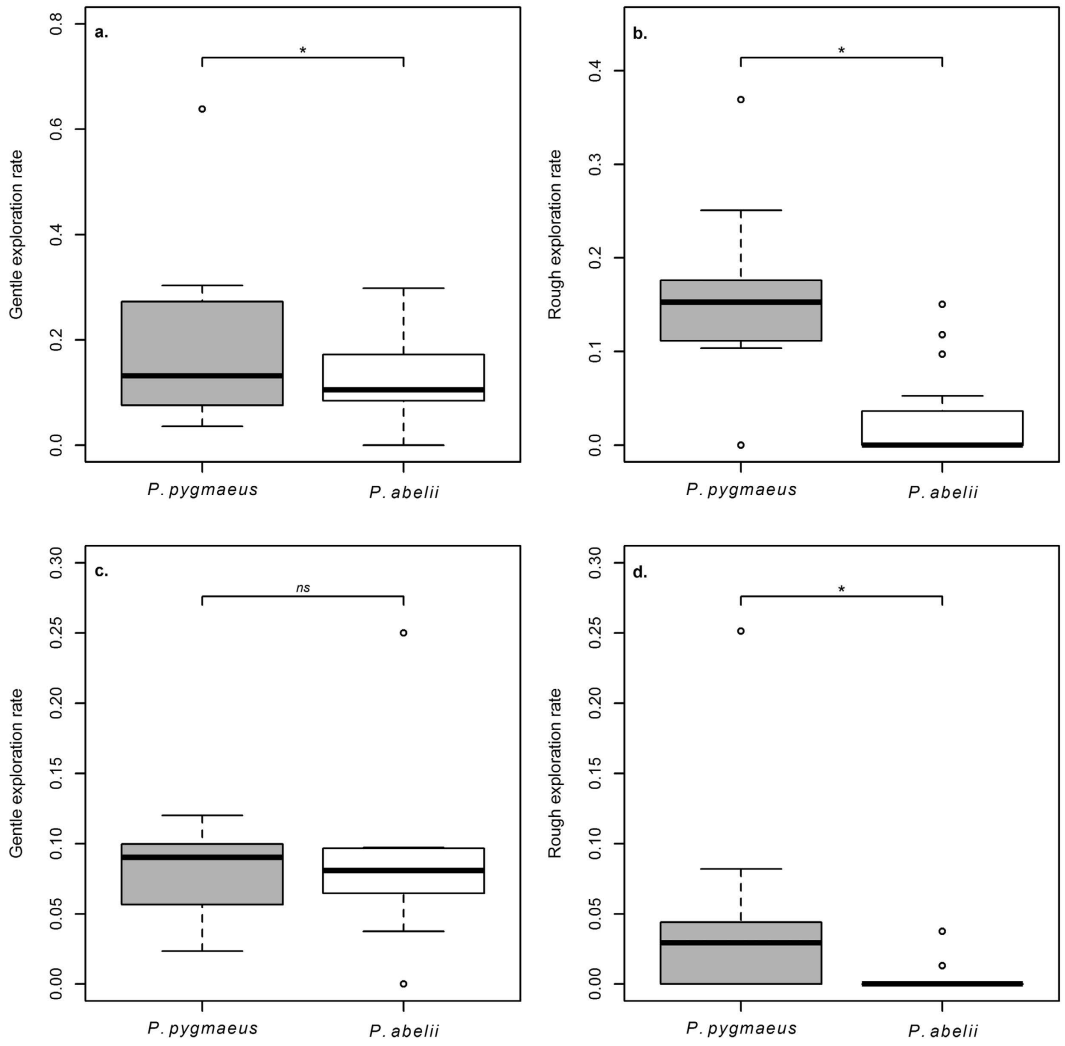

Figure 5. Exploration styles. Exploration rates (corrected for total time at apparatus): gentle exploration and rough exploration for both novel toy (**a**,**b**) (Gentle exploration: LM: $N_{Sumatra} = 19$, $N_{Borneo} = 9$, $P_{species} = 0.031$, $\beta_{species} = -0.163 \pm 0.071$, $P_{age} = 0.069$, $P_{sex} = 0.169$, rough exploration: LM: $N_{Sumatra} = 19$, $N_{Borneo} = 9$, $P_{species} < 0.001$, $\beta_{species} = -0.167 \pm 0.036$, $P_{age} = 0.636$, $P_{sex} = 0.155$), and detour reaching task (**c**,**d**) (Gentle exploration: LM: $N_{Sumatra} = 10$, $N_{Borneo} = 10$, $P_{species} = 0.648$, $P_{age} = 0.794$, $P_{sex} = 0.478$, rough exploration: LM: $N_{Sumatra} = 10$, $N_{Borneo} = 10$, $P_{species} = 0.042$, $\beta_{species} = -0.050 \pm 0.023$, $P_{age} = 0.301$, $P_{sex} = 0.134$).

the Borneans (Fig. 3). These results therefore support the existence of an intrinsic species difference in the ability to solve physical cognition tasks, in agreement with the prediction of the evolutionary version of the cultural intelligence hypothesis.

Given this clear difference in performance on tasks of physical cognition between these two closely related species, it is of great interest to identify possible underlying variables. We measured novelty response, inhibition and aspects of exploratory behaviour. Because Sumatrans were more cautious in tasting novel food (Fig. 4), better performance was not due to reduced neophobia, as was found in some previous studies[38,41]. The species difference was also not confounded by age effects. Although younger Sumatrans delayed their intake of novel food, when tested individually (Fig. 4b), the species difference remained even when we excluded the younger subjects from the Sumatran sample. Species with greater dependence on social learning have been suggested to also exhibit higher neophobia and conservative novelty response, because they strongly rely on social cues to engage in independent exploration[46]. However, captivity has been shown to suppress neophobia in orang-utans[47]. Therefore, it is remarkable that we still detect this species difference in a zoo comparison, suggesting a stronger predisposition for cautiousness in Sumatran orang-utans than Borneans.

In the honey tool-task, which consisted of multiple problem-solving steps, both species were equally keen on participating and spent equal time exploring the task (Supplementary Fig. S2), but Sumatran females, though not males, spent more time exploring the relevant parts of the apparatus (the holes containing honey; Fig. 6). Further, Bornean orang-utans were more likely to apply a rougher exploration style than their Sumatran relatives, both in the detour-reaching box and toward the novel toy (Fig. 5b,d). Such rough actions suggest that the subjects had

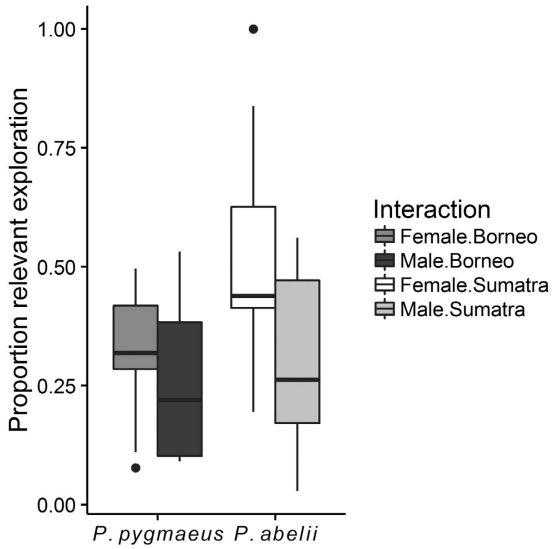

Figure 6. Relevant exploration. Proportion of relevant exploration time devoted to the honey extraction, corrected for total exploration duration of apparatus. Sumatran females spent more time exploring the relevant parts of the problem solving apparatus than Bornean, and males showed less relevant exploration time than females (LM: $N_{Sumatra} = 19$, $N_{Borneo} = 13$, $P_{species} = 0.064$, $\beta_{species} = 0.139 \pm 0.072$, $P_{age} = 0.210$, $P_{sex} = 0.029$, $\beta_{sex} = -0.183 \pm 0.080$).

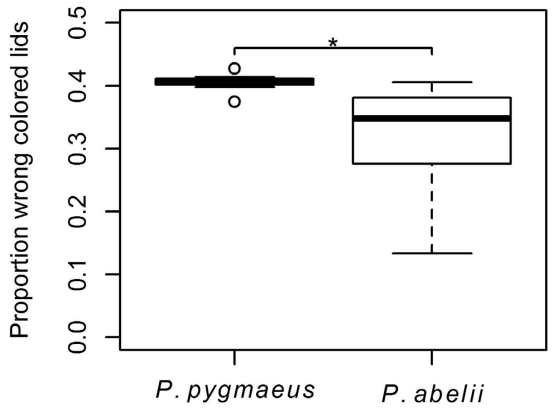

Figure 7. Reversal learning task. Proportion of lids opened of wrong colour corrected for total amount of lids touched in the reversal learning task. Sumatran subjects opened less wrong coloured lids than Bornean subjects, (LM: $N_{Sumatra} = 16$, $N_{Borneo} = 8$, $P_{species} = 0.011$, $\beta_{species} = -0.092 \pm 0.033$, $P_{age} = 0.899$, $P_{sex} = 0.475$).

given up on trying to find a solution and were either frustrated or attempting to reach the food reward through force, or both.

Reversal-learning tasks entail an element of inhibition[48]. A higher percentage of Sumatran individuals learned the colour reversal. Although this was not significant, we found that Sumatrans were also better at inhibiting their behaviour in that they opened significantly fewer lids of the wrong colour than Borneans (Fig. 7). Orang-utans have previously been reported to exhibit higher inhibitory control than other great apes[45], but our results suggest that Sumatrans show this even more than the Borneans, which complements their greater cautiousness and gentler explorative behaviour.

In sum, the superior cognitive performance by the Sumatran orang-utans may well reflect their greater inhibitory control and more cautious exploration style, which made them less likely to turn to destructive exploration and more likely to focus on relevant aspects of the problem at hand.

Because group size in the zoos examined did not affect the results and the zoos did not differ greatly in their enrichment regimes, this species difference cannot reflect any differences in opportunities for social or asocial learning during development other than those caused by innate differences in attention patterns or social tolerance by role models. Moreover, it is unlikely to be due to innate differences in the ability to effectively manipulate tools, because on Sumatra the tendency to use tools is limited to particular regions[32]. Zoo orang-utans of both

species use tools regularly and all nine zoos where the data was collected provided the apes with enrichment devices requiring stick tool-use, with which all subjects in our study were familiar.

If the species had been very different in overall or relative brain size, the same result would presumably have been obtained, given the effect of brain size on cognitive abilities in primates[49,50] and carnivores[51]. The study was designed to capture the effects of cultural intelligence at similar brain size. Nonetheless, there are minor brain size differences between the two orang-utan species. Although females are all approximately the same body size, those of the two western Bornean subspecies have a cranial capacity that is slightly (average 2–3%) smaller than that of the Sumatrans. However, those of the eastern subspecies *Pongo pygmaeus morio* have a cranial capacity that is on average 11–12% smaller than that of the other Bornean subspecies and 14% smaller than that of the Sumatrans[35]. However, because the breeding program in European Zoos that manages the population of *Pongo pygmaeus*, does not distinguish between subspecies, we do not know which individuals, if any, are of this subspecies, assuming there are any pure or hybrid *P. p. morio* at all in European zoos. Moreover, the brain size distributions between the species and subspecies show high overlap, and any difference in relative brain size is still less than that between the sexes of modern humans[52]. Furthermore, the greater interspecific variation in absolute and relative brain size among all great apes, relative to that found between Bornean and Sumatran orang-utans, does not translate into consistent differences in quantitative reasoning or inferential reasoning[53,54]. Most importantly, however, regardless of any residual effects of brain size, we identified plausible underlying causal differences in exploration style, which help us understand the species differences found here and may also be involved in species differences across a broader range of brain sizes (e.g. inhibitory control[55]).

This species comparison of physical cognitive tasks provides the first empirical confirmation of the cultural intelligence hypothesis in a non-human species, suggesting that the combination of more frequent opportunities for social learning and advanced skill repertoires have over evolutionary time produced cognitive differences between the two *Pongo* species. More generally, the traditional benefit hypotheses for the evolution of intelligence, such as the social brain hypothesis[56,57] or the technical intelligence hypothesis[58], both face the problem of grade shifts, i.e. that different lineages show major differences in intelligence in spite of similar social or technical challenges[24,59]. The cultural intelligence hypothesis, which basically argues that where learning is more efficient intelligence can be enhanced, may therefore be essential to complement the explanatory power of these benefit hypotheses.

Methods

Subjects. We undertook the study in nine European zoos (Table S1, supplementary material), where both species of orang-utans are housed under constant and similar conditions, and tested only mother-reared individuals. The European breeding program, EEP, holds all detailed information on birth dates, kinship, transfers and island of origin of all orang-utans in European zoos. Supplementary Table S1 describes the housing conditions and the time at which the experiments were run at each zoo.

During the cognitive tasks all subjects participated on their own initiative and individually, which controlled for variation in motivational state between subjects, albeit at the expense of a reduced sample size in some tasks. All tests were conducted either in the morning hours or around mid-day and all subjects were fed normally before and after participating in the tasks. The tasks were presented to the orang-utans in their smaller sleeping enclosures or directly in the large home enclosure, whenever a subject could be separated from the rest of the group there. If mothers could not be separated from their dependent offspring, they were tested together with their infants (the latter did not participate in the tasks). Participating subjects ranged in age from five to fifty-two years (Table S2, supplementary material). The average age was 17 years for Sumatran subjects, 21 years for Borneans. All tasks were video recorded with two SONY HDR-CX200 Handy cameras, because no humans were nearby or interacting with the subject during testing so as to minimize human impacts.

Ethical note. All experiments were purely behavioural and fully complied with the ethical guidelines of each zoo, the European Directive 2010/63/EU, and were approved by the ethics committee of the University of Zurich in Switzerland. Further, all data collected in the United Kingdom were approved by the British and Irish association for zoos and aquariums, BIAZA.

Description of physical cognition tasks. Inspired by the primate cognition test battery (PCTB) of Herrmann *et al.*[21] we developed a modified set of physical cognition tasks to assess different aspects of cognition. These tasks were modified because we wanted to make it possible to collect meaningful information without pre-training and frequent interactions with humans, and therefore had to make them as naturalistic and simple as possible, as well as adjust them to different locations of testing.

Detour reaching task. A large transparent plexiglas box (100 cm × 30 cm × 30 cm) was presented in the sleeping enclosure of the subjects. Because the box was placed inside the enclosure it was entirely accessible to the subjects to explore the whole box, providing suitable measurements of explorative actions. Exploratory actions of the plexiglas box were divided into two categories: rough (push, pull, hit) and gentle (touch, poke). The front side of the box had two openings, one small round hole (diameter 2 cm) and one large rectangular opening (30 cm × 20 cm) situated 50 cm from the small opening (Supplementary Fig. S1a). Before the subject entered the test enclosure a food reward (piece of fruit) was placed inside the plexiglas box right behind the small opening, through which the food reward did not fit. The subject would have to prevent its focus on the visible fruit in order to find the large opening and thereby the solution. Each subject was given five minutes to solve this task and the task started as soon as the subject approached to within one meter from the box. The moment the subject touched the fruit piece inside the box was counted as a successful solution and ended the task.

The honey tool-task. This problem-solving task presented a wooden box (50 cm × 80 cm × 5 cm) with two traps, which were covered with a plexiglas on the front side for visibility (Supplementary Fig. S1b). The upper trap was a straight, downward-sloping channel (30 cm × 5 cm) filled partly with honey, in which a 40-cm long stick was already inserted (and thus immersed into the honey). The second, lower trap was an L-shaped curve (15 cm × 10 cm), whose interior part, also filled with honey, could not be reached with a finger or a stick. We additionally provided two sticks (40 cm) and three bendable plastic ropes (20 cm) on the floor in front of the apparatus. In order to find the solution for the L-shaped trap, the subject needed to use one of the provided ropes as a tool and dip it into the L-shaped trap. The rope could also be explored as a tool in the straight trap but did not yield any honey reward due to its insufficient length. Likewise, the stick could not reach the honey in the L-shaped trap. The total time a subject was given for this task was ten minutes.

First, we assessed how attentive subjects were toward the test apparatus by calculating the time they spent within one meter of the apparatus as well as the duration of exploration of the apparatus. Exploration was defined as any event were the subject would touch and manipulate any part of the apparatus or the different tools provided right beside the apparatus, minus the time that was spent at performing the solution, e.g. dipping the stick into the straight trap. We also recorded relevant exploration events, which included all exploration events directed toward the two traps and not the apparatus itself (and thus relevant to the actual problem-solving). From this, we calculated the proportion of total exploration duration during which the subjects focused on relevant exploration. Second, for the cognitive performance we used four measurements from this task:

(a) Use of the information provided beforehand: re-use of the stick that was already provided as solution in the straight trap. The stick was counted as re-used if the subject did not let go of it, walked out of sight with it or put it on the floor before re-inserting it into the straight trap. A stick was defined as inserted if at least one third of the stick was inside the straight trap.
(b) Correct solution to the straight trap: if the subject did at any point during the ten minutes insert the stick to the straight trap, it was defined as a successful solution to the straight trap.
(c) Considering the rope as a tool: if the subject did at any point during the ten minutes tried the rope as a tool for either of the traps.
(d) Correct solution to the L-shaped trap: if the subject inserted the rope tool into the L-shaped trap during the ten minutes. Any act where a subject inserted the rope and thus recognized that the rope was the correct tool for the L-shaped trap was regarded correct solution, regardless of whether the subject actually obtained any honey.

The tube-trap task. The tube-trap task was also presented to each subject outside of the enclosure mesh, along with sticks to reach six horizontal metal tubes (Supplementary Fig. S1d). Each tube was 30 cm long and 5 cm wide, with an opening on either end, where the stick could be inserted to slide a visible reward (a piece of fruit or a nut) in two different directions. However, the tube had a trap, visible from the outside. Thus, if the reward was moved in the wrong direction it would fall down a 10 cm deep metal cylinder and get trapped. However, if the reward was moved in the correct direction it reached the end of the tube and fell out, to be picked up. The board contained six tubes. Each subject encountered the task in three consecutive trials, resulting in 18 possible attempts. Three tubes had the correct opening on the left side, three on the right side. Thus, if a subject would have a strong side preference and always slid the reward toward one side, it would reach nine correct out of 18 (50%). We therefore calculated the percentage of tubes an individual solved correctly and used a criterion of more than 60% of the tubes correct as a successfully solved task.

Reversal learning task. In this task the orang-utans were presented a wooden board, at a distance of ca. 20 cm outside of the enclosure mesh (Supplementary Fig. S1c). The board had 12 holes with 12 lids: six black and six white ones. The subjects were provided sticks to reach the lids of the board. In the first part of the task a food reward (fruit piece or nuts, depending on recommendations or preference of the keepers) was hidden behind either all the black or all the white lids (colour was randomly determined for each subject). We determined that the subject had successfully learned the association between right colour lid and food reward once at least five out of the six first lids it touched were of the correct (rewarded) colour. In addition, the subject had to pass an extra control trial to ensure it had learned the right association. After the control trial was also successful, we switched the position of the food reward to the opposite colour, and counted if and how many trials it took the subject to learn the reverse pattern. The task continued for four days and each subject was given three to four trials per day (depending on when a control trial was needed or not).

Novelty response tests. *Novel food.* As a novel food item we used potato mash that was coloured turquoise using regular food colouring and topped with a few black olives (Supplementary Fig. S1e). Each subject was then served a handful of the turquoise potato mash as a little pile on a board right outside the mesh of the test location. The novel food test lasted for a maximum of two minutes, but ended earlier in case all food had already been consumed. We measured the latency to taste the novel food as a proxy for cautiousness. We used the latency of tasting from the point when the subject first touched the item to control for potential differences due to the size of the enclosure mesh through which the subjects had to reach for the food items. As a control condition we also recorded reactions toward a familiar food item, which was either a fruit or vegetable that was part of the subjects' daily diet.

Novel toy. As a novel toy we presented the orang-utans with a wooden board containing three slits, in each of which sat two differently coloured tennis balls that could be rotated and moved in different directions

(Supplementary Fig. S1f). Subjects were given two minutes to interact with the novel toy. Since many zoo-housed orang-utans are familiar with tennis balls (albeit not with these colours or in this context), our intention for this task was to capture how they explore a new task that neither presents any particular problem to be solved nor produces a food reward. Explorative behaviour of the toy was divided into the same categories as for the detour-reaching task: rough- (bite, hit, pull, push) and gentle exploration (touch, poke, rotate, slide). We calculated exploration rates, counted as number of total exploration events of each category divided by the total time spent with the toy.

Statistical Analyses. The same observer (SF) coded all behaviour details from the videos of each task using Mangold Interact 9.7. The sample size for each task varied somewhat, because zoos differed slightly in opportunities for separate testing and not all individuals could always be separated. To test for a potential species difference in overall performance (task solved: yes/no), we fitted a Generalized Linear Mixed-effects Model (GLMM) with a binomial error distribution to the data. We incorporated species as the main fixed effect, while task identity, age, sex, group size, and the number of zoos the subject had lived in over the course of its life-time, were included as additional (confounding) fixed effects. Planned contrasts for task (the only categorical predictor with more than two levels) were set to compare a subject's performance on each task to its performance on the detour-reaching task (i.e. the task with the highest overall performance, solved by all but 2 subjects). We controlled for repeated observations on each task across the same subjects from different zoos by specifying task identity and individual identity nested within zoo as two crossed random effects. For the exploration data of each task (time to solution) we used standard linear models, with species as independent variable while controlling for age and sex. All statistical analyses were conducted in R version 3.2.3, using the "lme4" package[60].

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Acknowledgements

We thank all the following zoological gardens for their collaborations and contribution to our study: Zoo Dortmund, Twycross Zoo, Durrell Wildlife Trust, Allwetterzoo Münster, Zoo Basel, Apenheul Primate Park, Wolfgang Köhler Primate Center at Leipzig Zoo, Blackpool Zoo and Paignton Zoo. Special thanks to all the zoo keepers who helped with the experimental set ups. We are grateful to Daniel Haun, Katja Liebal and Judith Burkart for their feedback and inputs while developing the set of experimental task. We also express our gratitude to the following foundations who have financially supported this project: A. H. Schultz Foundation, Paul Schiller Foundation and the Claraz Foundation in Switzerland and Waldemar von Frenckells Foundation, Ella and Georgh Ehrnrooths Foundation, Otto A. Malms Donationsfond, Nordenskiöld Samfundet and Oskar Öflunds Foundation in Finland.

Author Contributions

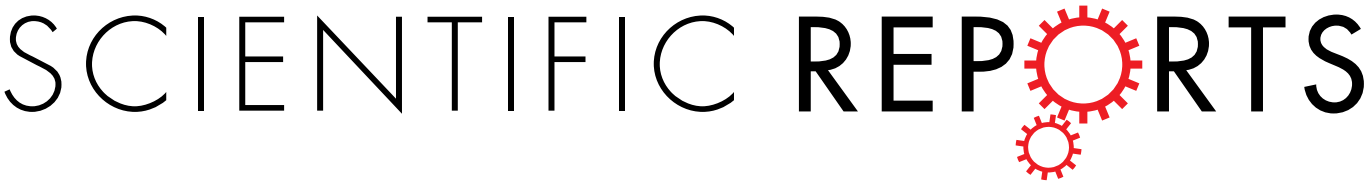
S.I.F.F. conducted the study and wrote the paper. E.W. performed statistical analyses. JP supervised part of the data collection and commented on the manuscript. CV supervised the project.

Additional Information

Supplementary information accompanies this paper at http://www.nature.com/srep

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Forss, S. I. F. *et al.* Cognitive differences between orang-utan species: a test of the cultural intelligence hypothesis. *Sci. Rep.* **6**, 30516; doi: 10.1038/srep30516 (2016).



OPEN

Orientation toward humans predicts cognitive performance in orang-utans

Received: 11 August 2016
Accepted: 30 November 2016
Published: 09 January 2017

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Non-human animals sometimes show marked intraspecific variation in their cognitive abilities that may reflect variation in external inputs and experience during the developmental period. We examined variation in exploration and cognitive performance on a problem-solving task in a large sample of captive orang-utans (*Pongo abelii* & *P. pygmaeus*, N = 103) that had experienced different rearing and housing conditions during ontogeny, including human exposure. In addition to measuring exploration and cognitive performance, we also conducted a set of assays of the subjects' psychological orientation, including reactions towards an unfamiliar human, summarized in the *human orientation index* (HOI), and towards novel food and objects. Using generalized linear mixed models we found that the HOI, rather than rearing background, best predicted both exploration and problem-solving success. Our results suggest a cascade of processes: human orientation was accompanied by a change in motivation towards problem-solving, expressed in reduced neophobia and increased exploration variety, which led to greater experience, and thus eventually to higher performance in the task. We propose that different experiences with humans caused individuals to vary in curiosity and understanding of the physical problem-solving task. We discuss the implications of these findings for comparative studies of cognitive ability.

Human intellectual performance is known to be strongly affected by developmental inputs[1–3]. However, similar effects in nonhuman primates have received far less attention. So far, the possible effect of experience on cognitive abilities in non-human primates has mainly been studied by examining the two extreme cases of deprivation and enculturation. Physical and social deprivation have been reported to cause strong negative outcomes on cognitive development in primates; especially maternal separation has been shown to result in both short- and long-term socio-cognitive consequences[4–11]. The opposite extreme in rearing environment is enculturation. Especially among great apes, enriched socio-cultural inputs, in the form of extensive interactions with humans, result in enhanced physical cognitive skills[12–14] (see also ref. 15), but particularly in improved socio-cognitive and communicative abilities[16–20]. Both deprivation and enculturation therefore demonstrate that extreme social influences shape the cognitive abilities of nonhuman primates.

Even without being deprived or enculturated, captive primates also show intraspecific variability in cognitive abilities[21,22], but the sources of this variability remain largely unstudied and it remains unclear whether the same social processes are involved. In particular, we don't know to what extent variable rearing histories affect cognitive performance across individuals under non-extreme conditions, and if so whether they do so through their effect on psychological variables such as motivation to solve problems, responses to novelty and exploration style.

The aim of the present study was, first, to examine in a sample of more than 100 captive orang-utans (*Pongo abelii* and *P. pygmaeus*) how variation in captive management regimes and individual rearing histories affects psychological variables, such as human orientation, motivation and exploration style, and second, to examine whether these factors explain variation in cognitive performance in a tool-use task. Our sample contained

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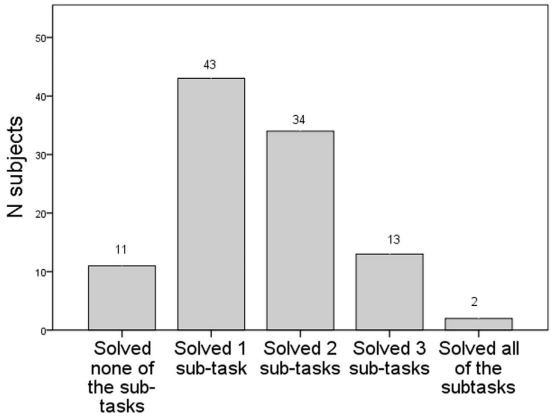


Figure 1. Honey tool-task performance. Frequency of subjects that solved zero to all subtasks.

orang-utans from a wide range of rearing backgrounds: both zoo groups, including mother- and hand-reared individuals, and individuals housed in rehabilitation stations who were wild-born but subsequently experienced captivity for variable periods of time, some as pets, before entering the rehabilitation station. Importantly, the individuals were all currently kept in captivity, allowing similar individual testing conditions. This provided us with an excellent opportunity to test the strength of the long-term effects of early rearing conditions on exploration styles and cognitive performance.

Because our sample included individuals from both zoos and rehabilitation stations, we could also test the independent effect of current housing conditions. Zoos and rehabilitation stations differ in their purpose of holding captive apes. Zoo apes have lived all their lives in a similar and stable environment, mostly together with their mothers and in intense contact with both knowledgeable conspecifics and human caretakers, with additional exposure to human strangers on a daily basis. Virtually all zoos also offer additional enrichment in the form of various foraging activities. In rehabilitation stations the purpose is very different. Some individuals may have experienced traumatic events in their past (capture and loss of mother, sometimes accompanied by injury) and thus need to recover physically and mentally. The stations' ultimate aim is to return individuals to the wild. They consequently avoid bringing about a too close attachment to humans or exposing them to artificial enrichment devices. Moreover, most rehabilitating apes lack the close bond to their mother and are instead housed in peer groups.

Reactions to an unfamiliar human have previously been used to measure temperament in great apes[23] and physiological distress responses in monkeys[24,25]. In order to estimate the underlying psychological consequences of human-related experiences that might explain variation in exploration and cognitive performance, we developed a new measure, the human orientation index (henceforth: HOI; see Methods for details). This measure was developed because the effect of captivity on cognitive abilities[26,27] seems to reflect a major psychological change. First, because in multiple species, reduced neophobia has been shown to influence problem-solving skills[28–31], and because captive orang-utans show strongly increased interest in novel items relative to their wild counterparts[32] (as do other species[27,33]), we assessed the response to novelty across individuals with different captive experiences. Second, because the effect of captivity on cognitive performance is particularly pronounced in the context of tool use[34–39], we assessed cognitive performance using a novel tool-use task including multi-step problem-solving with high ecological validity: the honey-tool task. In order to prevent variation in human orientation from confounding cognitive performance during the testing, no humans were present during the tests, which were video-recorded.

Results

Cognitive performance. For the honey tool-task, we found large variation in cognitive performance among the 103 orang-utans (Fig. 1). Eleven individuals did not solve a single sub-task. The modal and median score on total performance was 1 out of a maximum of 4. The four different cognitive measurements of the honey tool-task varied significantly in difficulty. In order to examine whether the ability to solve the different sub-tasks was cumulative, we applied a Guttman scale, which showed a reproducibility coefficient of close to one (0.97). This strongly suggests that the ability to solve the more difficult sub-tasks was nested within the performance of the other sub-tasks: 90% of the 103 individuals performing the honey tool-task fitted the applied Guttman scale of the four different sub-tasks (see Methods and Fig. 2 for details). As expected, 'remove stick' was the easiest, 'insert the stick in the straight channel' was next, followed by 'making a tool', whereas 'inserting the rope in the curved channel' was most difficult (Fig. 2, Sub-task) for the orang-utans in this study. Due to this variation in difficulty, we treated the four levels of cognitive performance as an ordinal variable in further analyses.

We next tested whether background and housing conditions, species, sex, and age could explain the variation in cognitive performance on the honey tool-task. Table 1 shows the results of a binomial Generalized Linear Mixed Model (GLMM) of the honey tool-task performance, with the response variable being whether or not a subject solved each sub-task. The GLMM allowed us to control for repeated observations in each facility and on each individual. The results revealed that the human orientation index (HOI) was a good predictor of the ability to solve the task ($B \pm SD = 0.227 \pm 0.08$, $Z = 2.699$, $P = 0.007$; Table 1), as was the latency to touch unfamiliar

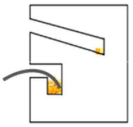
Image	Graphic	Task measurement	Definition	Remarks
		Remove stick	Stick provided in the straight channel is taken out	Recognition of the stick in the channel and removal of it
		Insert stick in straight channel	Any of the three sticks are inserted into the straight trap during the 10 minutes test time	Understanding of stick fitting the straight trap
		Tool manufacture/ other tool use	Any tool (stick or rope) is modified or any other material is used as a tool in any of the channels	Innovative attempt to retrieve honey by modifying existing tool or trying out any other solution
		Insert rope in L-curved channel	Any of the three ropes are inserted into the L-shaped channel	Understanding of the properties of rope fitting the L-shape channel

Figure 2. Overview of the design, structure and measurements of cognitive performance. The honey tool-task offered two problems to solve: an upper channel with a stick solution and lower channel with a rope solution.

	B	*SE*	*Z*	*p value*
(Intercept)	−2.588	1.33	−1.943	0.052
Human Orientation Index	0.227	0.08	2.699	**0.007****
Novel food: time until touch	−0.034	0.01	−2.263	**0.024***
Novel object: time until touch	−0.025	0.01	−2.123	**0.034***
Novel object: exploration duration	0.003	0.01	0.433	**0.665**
Age	−0.006	0.03	−0.232	0.817
SEX (male)	0.124	0.51	0.243	0.808
Species (Sumatra)	−0.094	0.59	−0.16	0.873
Background				
Wild vs. Rest	−0.173	0.27	−0.639	0.523
Rehab vs. Zoo	−0.402	0.29	−1.395	0.163
Unknown vs. Rehab.Rest	0.073	0.20	0.367	0.714
Human vs. Station (within rehabilitation station)	−0.479	0.48	−1.008	0.314
Mother vs. Hand (within zoo)	0.365	0.51	0.722	0.470
Accessibility (trend analysis)				
Linear	0.786	0.76	1.04	0.298
Quadratic	0.228	0.89	0.257	0.797
Cubic	−0.189	0.89	−0.213	0.831
Sub-task (trend analysis)				
Linear	−4.969	0.74	−6.737	**<0.001*****
Quadratic	1.554	0.44	3.559	**<0.001*****
Cubic	−0.205	0.33	−0.626	0.531

Table 1. Generalized Linear Mixed Model of overall performance in the honey tool-task. Note: The model is controlling for repeated observations on each facility and individual. The performance in the honey tool-task was binary measured. The Analysis included 88 individuals in 9 different zoos/rehab stations, totalling 352 observations, $\chi^2 = 226.27$, $P < 0.001$, P-values below 0.05 appear in bold. Parameter estimates from a binomial GLMM, predicting the probability of an animal solving the task.

food ($B \pm SD = -0.034 \pm 0.01$, $Z = -2.263$, $P = 0.024$; Table 1) and a novel object ($B \pm SD = -0.025 \pm 0.01$, $Z = -2.123$, $P = 0.034$; Table 1). The less neophobic the individuals, the more likely they were to solve the task. When we removed the novelty responses from the analysis, the HOI remained the main predictor of performance (Table S1, supplementary material). Because an individual's age and the time it had spent in captivity were strongly correlated, only the factor age was considered for the analysis, but it did not influence task performance. Subtle differences between enclosures, which might affect the ease of access to the apparatus, were controlled for in the analysis, but again did not contribute to explaining the variation in cognitive performance. Perhaps surprisingly, none of the other possible variables (sex, species [Sumatran or Bornean], and the various background and current housing conditions of the orang-utans) predicted performance; they also had no influence on task performance when HOI was excluded from the analyses (Table S2, Supplementary material).

Exploration behaviour underlying cognitive performance. The orang-utans' performance on the tool-use task was best accounted for by exploration variety, which explained 27% of the variation (Figs 3b and 4),

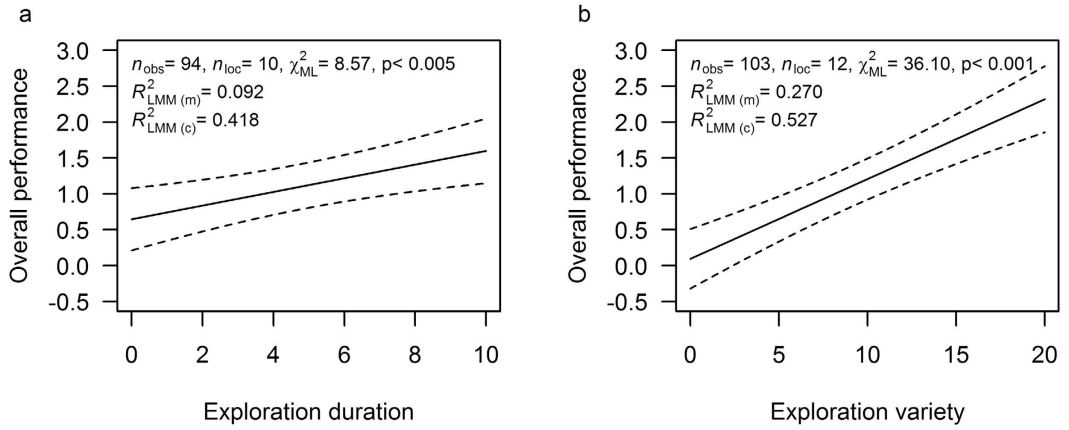


Figure 3. The relationships between exploration behaviour and the overall cognitive performance. (**a**) Overall performance in relation to the exploration duration. Individuals that explored longer were significantly better problem solvers ($N_{obs} = 94$, $N_{location} = 10$, $\chi^2_{ML} = 08.57$, $P = 0.005$). (**b**) The overall task performance in relation to the total variety of exploration actions ($N_{obs} = 103$, $N_{location} = 12$, $\chi^2_{ML} = 36.10$, $P < 0.001$).

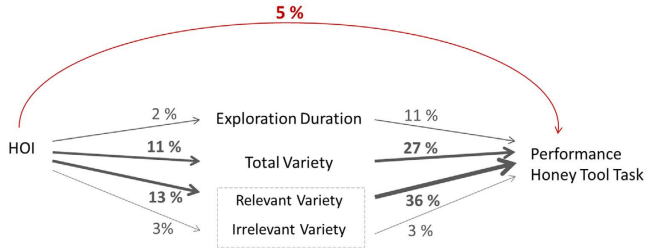


Figure 4. Graphical illustration of the relationship between the human orientation Index (HOI), the cognitive performance and exploration duration and variety, in context to each other. The total variety can be divided into relevant and irrelevant variety. The figure also indicates the percentage of variation estimated by the pseudo R^2 for linear mixed effects margins that is explained by each factor. The thickness of the arrows accentuates the strength of the influence.

whereas exploration duration predicted 9% of the variation ($N_{obs} = 94$, $N_{location} = 10$, $\chi^2_{ML} = 08.57$, $R^2_{LMM(m)} = 0.092$, $P = 0.005$, Figs 3a and 4). However, the HOI only explained 5% of cognitive performance ($\chi^2_{ML} = 6.21$, $P < 0.05$).

The effect of human orientation on exploration. A Linear Mixed-Effects Model (LMM) analysis of the subjects' exploration of the apparatus, which controlled for repeated measurements in each facility, showed that HOI accounted for 11% of the variation of the total exploration variety ($N_{obs} = 94$, $N_{location} = 10$, $\chi^2_{ML} = 12.02$, $R^2_{LMM(m)} = 0.1113$, $P < 0.001$, Figs 4 and 5b). In addition, there was a trend showing that individuals with a higher HOI explored the apparatus longer than those with a lower HOI ($N_{obs} = 94$, $N_{location} = 10$, $\chi^2_{ML} = 3.53$, $R^2_{LMM(m)} = 0.025$, $P = 0.06$, Fig. 5a), although the HOI explained a mere 2% of the variation in exploration duration (Fig. 4). This low proportion is not surprising, because the most successful orang-utans, and thus the ones with high HOI values, stopped exploring once they found the solution to the problem and spent their remaining time extracting honey.

Random exploration of the apparatus per se does not necessarily raise the chances of finding the solution. Individuals who can distinguish between relevant and irrelevant parts of the apparatus should be more successful (Supplementary Table S3). We therefore also investigated the separate effects of exploration variety directed at the relevant or irrelevant areas of the apparatus. We calculated marginal pseudo-R^2 values to estimate the proportion of variation explained by the fixed effects in our model. The HOI explained 13% of the variation of relevant exploration ($\chi^2_{ML} = 13.67$, $P < 0.001$, Fig. 4 and Supplementary Table S4), which subsequently accounted for 36% of the variation in cognitive performance. In contrast, HOI explained only 3% of the irrelevant exploration ($\chi^2_{ML} = 2.93$, $P = 0.087$, Fig. 4), which accounted for only 3% of performance in the task. The effect of a higher HOI was thus primarily on the amount of exploration and especially on the diversity of exploration on relevant parts of the task, with the latter explaining 36% of cognitive performance. Furthermore, neither housing- nor background/ rearing history had any effect on the exploration of the apparatus (Supplementary Table S4).

Additionally, using a Linear Mixed-Effect Model (LMM), controlling for each subject's housing location, we compared the exploration style of the most successful individuals, the 10 subjects who solved the most difficult problem of 'inserting the rope in the curved channel' ('ropers'), to the other non-successful individuals ('non-ropers'). There was no difference in exploration duration between ropers and non-ropers. However, the ropers differed significantly from non-ropers in their exploration variety ($P = 0.012$). Ropers not only showed a

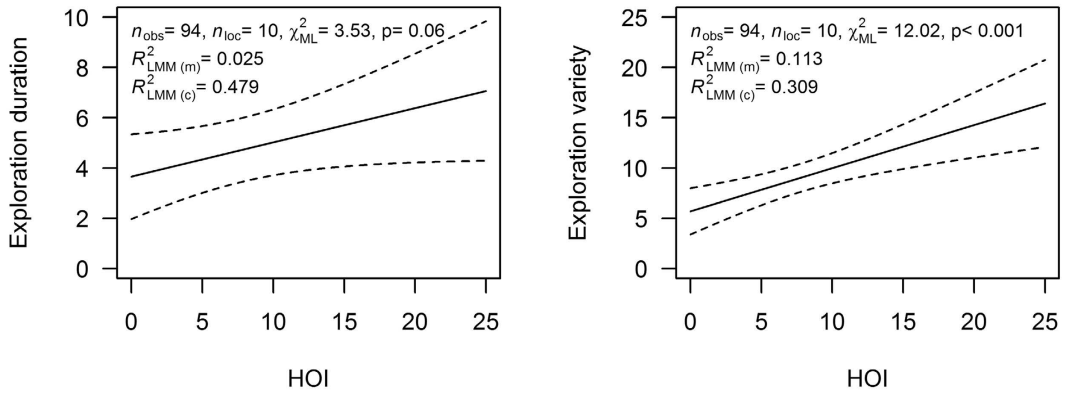


Figure 5. The relationships between the human orientation index (HOI) and exploration behaviour showed significant dependencies in Linear-Mixed-Effect-Models (LMM) that controlled for repeated observations in each facility. (**a**) Exploration duration in relation to HOI-index ($N_{obs} = 94$, $N_{location} = 10$, $\chi^2_{ML} = 3.53$, $R^2_{LMM(m)} = 0.025$, $P = 0.06$). (**b**) Total variety of exploration actions in relation to the HOI ($N_{obs} = 94$, $N_{location} = 10$, $\chi^2_{ML} = 12.02$, $R^2_{LMM(m)} = 0.1113$, $P < 0.001$).

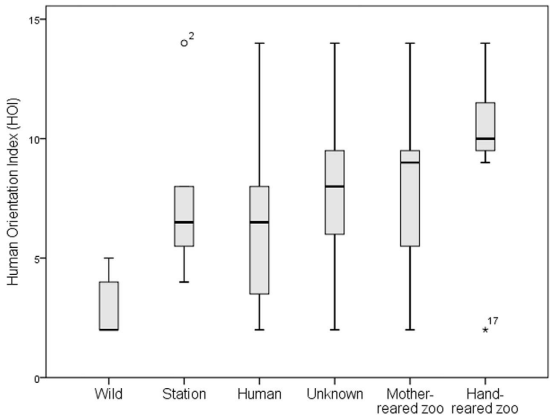


Figure 6. The human orientation index (HOI) in relation to background history. Groups of individuals with different background histories differed slightly in their human orientation.

greater diversity of explorative actions, but also a far greater diversity of exploration on relevant parts of the apparatus ($p < 0.001$; note that solving the rope solution is itself not counted as relevant exploration). Moreover, the ropers' HOI was 29.7% (and significantly) higher than that of non-ropers ($\chi^2_{ML} = 4.06$, $P < 0.05$).

Evaluating the human orientation index. Given the large effect of the HOI on exploration style, we examined whether the different background categories determined an individual's human orientation index. 'Wild' individuals strongly diverged from any other category in that they took longer or did not respond at all to the novel food and novel object (Supplementary Fig. 1) and by showing significantly lower HOI values (Kruskal-Wallis test: $N = 95$, $P = 0.002$, Fig. 6). However, pairwise comparisons of each background category (controlling for age, sex and species as well as repeated observations from each study location and correction of P-values for multiple comparisons using Tukey) revealed no significant differences in HOI between the background categories (Supplementary Table: S5).

The reaction toward novel humans might also be the result of several other factors, such as a response to any novelty or to social beings (human or orang-utan). Therefore, we also examined the links between HOI and the three novelty response experiments (concerning novel food, novel objects and novel conspecifics). Results of a Linear Mixed-Effects Model (LMM) evaluated the relation between the HOI and two other novelty response tasks, the novel-object and the novel-food task. The HOI was not explained by the latency to touch either the novel food ($B \pm SD = -0.057 \pm 1.12$, $df = 78.83$, $t = 6.401$, $P = 0.332$; Table 2) or the novel toy ($B \pm SD = 0.008 \pm 0.02$, $df = 81.9$, $t = 0.457$, $P = 0.649$; Table 2), whereas the latter two were correlated (Spearman's rho: $r = 0.314$, $N = 98$, $P = 0.002$, 2-tailed). Neither did the exploration duration of the novel toy explain the variation in HOI ($B \pm SD = 0.006 \pm 0.01$, $df = 81.99$, $t = 0.584$, $P = 0.561$; Table 2). Thus, the HOI did not simply reflect a positive response to novelty per se. To test whether the HOI represents a general interest in social beings, and thereby a higher social motivation in general or whether it describes the interest in humans specifically, we performed an additional social-interest-task with a subset of individuals of one rehabilitation station ($N = 28$, see Method section). The HOI did not seem to measure

	Estimate	*SE*	*df*	*t value*	*p value*
(Intercept)	7.155	1.12	58.15	6.401	<0.001***
Novel food					
Latency touch	−0.057	0.06	78.83	−0.977	0.332
Novel Object					
Latency touch	0.001	0.02	81.9	0.457	0.649
Exploration duration	0.006	0.01	81.99	0.584	0.561

Table 2. Linear Mixed-Effects model of the Human Orientation Index controlling for repeated observations on each facility. *Note: N observations = 85, N place = 9,* $X^2_{ML} = 3.556$, $P = 0.314$, P-values below 0.05 appear in bold.

a general social interest, since the duration spent in close proximity to a novel human did not correlate with the time spent in close proximity to novel conspecifics (Spearman's rho: r = 0.198, N = 28, P = 0.312, two-tailed).

Discussion

This study represents one of the largest systematic individual-level comparisons of cognitive tool-using abilities in apes, involving 13 different captive groups in both zoos and rehabilitation stations in which none of the individuals were deprived or enculturated. As expected, the latency to touch novel food or objects, and thus reduced neophobia, was an important independent predictor of task performance (Table 1), as has been found in other studies[28–31]. However, we also found that variation in problem-solving skills in the honey tool-task was equally predicted by persistent and varied explorative behaviour, which in turn was highly influenced by the orang-utans' psychological orientation as assessed with the human orientation index, HOI (Table 1). We suggest the following biologically most plausible causal cascade, backed up by a series of analyses: Human orientation mainly influenced both the orang-utans' motivation to explore and the nature of their exploration, and consequently affected their understanding of the problem-solving task, and thus their success in solving it.

The reaction towards humans could have several dimensions, other than the mere interest in humans, and our results allowed us to characterize the nature of the Human orientation Index (HOI) in more detail. A high HOI does not simply reflect the expectation of food that is provided regularly by humans, because HOI varied extensively and all these orang-utans depended on humans for their food. The different background categories also showed higher variability in their HOI than in their novelty response (Fig. 6 and Supplementary Fig. S1). Moreover, if it were mere food expectation, variation in HOI should be associated with caretakers that provide the daily food supply rather than random strangers. Finally, the HOI does not reflect general novelty response or general social interest, as it was not correlated with the approach latency to novel food nor objects (Table 2), nor with interest in novel conspecifics. Therefore the effect was human-specific and increased the motivation to explore, expressed as increased duration and variety of exploration (Fig. 5a and b).

The HOI thus captures a fundamental psychological change that is induced by human contact. The different background categories overlapped largely in their HOI (Supplementary Table S5), implying that each individual's specific nature and experience of human contact is more influential than the human exposure time per se. However, our sample included a few wild individuals who had spent their whole immature period in natural habitat and showed very low human orientation compared to most other conspecifics housed in zoos and rehabilitation stations, independent of the time they had spent at the station (Fig. 6). This indicates that the change caused by humans can only happen at an early age, suggesting a sensitive period for social inputs. Since this kind of psychological orientation is absent in nature[32], we can ask which natural process is being mimicked or modified by human contact. The answer is remarkably simple: humans replace the role of the mother and other conspecific experts, and the rich variety of artefacts provided by humans enriches their physical environment. In their natural niche, orang-utans as well as other primates are prone to attend to their mother and other expert conspecifics and learn necessary skills socially[40–45]. Exploration plays a crucial role in skill acquisition in the wild, but virtually all exploration is socially facilitated, allowing orang-utans to overcome intrinsic neophobia[32].

Given the identification of human orientation, rather than rearing conditions, as the key determinant of cognitive ability in captive apes, it makes sense to revisit the role of deprivation and enculturation. Because deprivation involves the complete loss of any role models, whereas enculturation involves the presence of far richer social inputs by more actively engaged role models than under normal conditions, one could argue that the degree of human orientation may largely explain the whole spectrum of cognitive performance among great apes. This perspective also explains why enculturated apes outperform others not just in socio-cognitive skills, but also in physical cognitive skills[19,46].

The social triggering of the engagement with artefacts is highly influential in human child development[47,48].

Studies within the field of comparative psychology have documented non-human primates' tendency to attend to humans[17,49] and acknowledged the improvement in learning cognitive tasks due to human contact in captive settings[50,51]. Systematic species comparisons of primates' attention structure toward humans are rare. Nonetheless, in 1916, Yerkes[52] already suggested that the qualitatively better cognitive performance of an orang-utan compared to monkeys was due to the ape's social attention to human actions. Our results thus support previous suggestions[39,53,54] that early exposure to humans and human artefacts presents a broader range of opportunities for exploration resulting in increased innovativeness in captive apes. Over time, the accumulating experience resulting from attention to humans leads to improved problem-solving ability, provided the exposure to humans is early in life. In conclusion,

Study Facility	N	Species	Age Range	Social Housing	Test Location	Time Period
Zoo 1	6	*P. pygmaeus*	6–43	Mixed-age group	Sleeping quarter	Apr-May 2013
Zoo 2	8	*P. pygmaeus*	13–52	Mixed-age group	Sleeping quarter	Jan-Feb 2014
Zoo 3	4	*P. abelii*	5–13	Mixed-age group	Smaller enclosure	Nov 2013
Zoo 4	4	*P. pygmaeus*	13–31	Mixed-age group	Sleeping quarter	Jan 2015
Zoo 5	4	*P. abelii*	8–23	Mixed-age group	Sleeping quarter	Nov-Dec 2012
Zoo 6	5	*P. abelii*	9–49	Mixed-age group	Sleeping quarter	Mar 2013
Zoo 7	6	*P. abelii*	5–25	Mixed-age group	Test enclosure	Mar 2014
Zoo 8	2	*P. pygmaeus*	18–20	Mixed-age group	Sleeping quarter	Feb 2015
Zoo 9	2	*P. pygmaeus*	14–36	Mixed-age group	Sleeping quarter	Jan-Feb 2013
Rehab. Station 1	5	*P. abelii*	3–6	Solitary	Home enclosure	Apr-Jun 2013
Rehab. station 2	18	*P. pygmaeus*	6–17	Solitary	Home enclosure	May-Jun 2014
Rehab. station 3	28	*P. pygmaeus*	8–14.5	Peer group	Test enclosure	June-Sep 2012
Rehab. station 4	11	*P. abelii*	5–25	Solitary	Home enclosure	Oct 2012–Mar 2013

Table 3. Overview of subjects and facilities.

human orientation at least partly explains the phenomenon that captive primates that are exposed to both conspecific and human role models experience increased opportunities for socially induced exploration and learning (cf. ref. 55).

Our detailed analyses revealed that the HOI influenced an individual's duration and especially its variety of exploration (Fig. 5a and b), which subsequently explained cognitive performance (Fig. 3a and b, Fig. 4). Previous studies on hyenas[29] and birds[56] have also reported that the diversity of exploration actions influences innovativeness and problem-solving skills. However, in our study, individuals with a strong human orientation were more successful in the task, not only through their exploration diversity, but also by focusing on the relevant parts of the apparatus (Fig. 4), implying that they were better at recognizing the actual challenge presented in the honey tool-task. Importantly, these parts were relevant not because they directly led to the solution, but rather because exploration of these parts improved the animals' understanding of the physical properties of the problem. For example, individuals that traced the honey channel from the outside of the glass obviously understood that there is honey inside, but were at that time not searching at the correct part of the apparatus, the channel entrance. Similarly, individuals poking with their finger into the curved channel may have gathered information on its length. Exploration can therefore be viewed as latent learning: it allows an animal to gather knowledge of the texture, the material, and the problem itself. Over time, then, individuals with a high HOI will gain more experience, which contributes to their focus on relevant aspects of the problem and hence problem-solving success.

The effects of the HOI on problem-solving success may have been so strong that they masked the effects of other factors. Thus, we found no differences between the two orang-utan species (*P. abelii* and *P. pygmaeus*), even though these were found when orang-utans with very similar backgrounds (all mother-reared zoo individuals) were compared on a range of cognitive tasks[57].

This study documented strong effects of human orientation on problem-solving abilities, through its effects on response to novelty, motivation to explore, exploration persistence and ultimately experience. This finding suggests that it is just as impossible to design culture-free cognitive tests for primates as it is for humans. In this sense, tests of primate cognition are inevitably deeply anthropomorphic. However, once we have controlled for the subjects' human-related histories and given that problem-solving ability is about dealing with unknown, novel problems the variation captured in these tests nonetheless reflects variation in intrinsic cognitive abilities and should be comparable within and across species. Therefore, we suggest the HOI may be a useful tool in standardizing comparisons across primates, especially studies concerning ape subjects with various background and human-related experiences. In future work, we will further disentangle the exact nature and causes of the HOI and address additional problem-solving domains.

Methods

Subjects and study facilities. Our total sample size involved 103 orang-utans: 68 *Pongo pygmaeus spp* and 35 *Pongo abelii* (Supplementary Table S6). Data collection on the zoo-housed sample took place at nine different European zoos between November 2012 and January 2015; all zoo data was collected by SF (Table 3). In total the zoo sample consisted of 41 individuals, of whom 31 were mother-reared and 10 whose own mother had either died or rejected the infant and were therefore hand-reared. They were cared for by human caretakers, within the zoo or partly within a human household, and subsequently returned to a group of zoo-living conspecifics (Table 4).

Data on 62 rehabilitation orang-utans were collected between June 2012 and June 2014 by LD and ZK, supported by a trained assistant, Andreas Wendl. In Borneo data collection took place at two rehabilitation stations, both situated in Central Kalimantan (Table 3). In Sumatra data collection took place at two sites of the same station: the quarantine station and at the release site (Table 3).

Depending on available background information the sample collected at the rehabilitation stations was further divided into the following groups: Wild, Station, Human and Unknown. Individuals were assigned to these four groups depending on the estimated age at arrival at a rehabilitation station (based on tooth eruption patterns) and their previous history with humans (Table 4). Table 4 shows that infants are usually caught when very young because then they are still easy to handle and thus most attractive as pets.

Background during early development	N	Age Range (years)	Current Housing	Years in Captivity	Human Exposure	Remark
Wild	5	10–25	Rehabilitation station	0–7	Minimal	Majority of life in natural habitat. Arrived at a rehabilitation center as adolescents or adults, eventually to be translocated to a new natural habitat.
Station	8	5–11	Rehabilitation station	4–10	Mainly human raised.	Minimum 80% of life in rehabilitation station. Arrived at station as dependent offspring at the age of 1.5 year or younger.
Human	16	3.5–14	Rehabilitation station	0–9	Minimum 6 months with humans	Arrived at rehabilitation station older than 1.5 years of age. Background history with human contact (minimum 6 months), e.g. pet
Unknown rehab	33	3–17	Rehabilitation station	0.5–14	Unknown before arrival at station	No background information. Arrived at station between 2 and 7 years of age and spent possibly large part of the developmental phase in captivity.
Mother-reared Zoo	31	5–52	Zoo	Whole life	All life within human care	Nursed by own mother within a zoo. All life in captivity with exposure to human caretakers and visitors.
Hand-reared Zoo	10	13–43	Zoo	Whole life	Human hand nursing and all life within human care	Nursed by human caretakers either at the zoo or in human households. All life in captivity with exposure to human caretakers and visitors.

Table 4. Categories of subjects and their background histories.

Housing conditions. In the zoos, individuals were housed in mixed-aged groups of conspecifics ranging from four to 12 individuals in standard indoor enclosures during the day, and mostly separated individually or in pairs into sleeping quarters for the night. Most zoos also provide the orang-utans with a larger outdoor enclosure. At each zoo, animal keepers are in daily close contact with the orang-utans, providing them with food but also with diverse enrichment activities. Zoo visitors were additionally in daily visual contact with the orang-utans.

In the rehabilitation stations the housing situations were more heterogeneous (see Table 3). They differed according to the standards and capabilities of each facility and the age, sex and background of the individuals. All orang-utans in this study were held in solitary enclosures at the time of the study, except for one station housing 28 individuals socially in groups of 2–6 individuals. In general contact with humans was reduced to caretakers cleaning and feeding several times a day and veterinary care as needed. Each enclosure had simple enrichment devices, such as ropes, and several times a week the subjects received extra food-related enrichment or leafy branches. In some facilities, small infants lived in a nursery with other orang-utan infants and human caretakers serving as replacement mothers. These infants had daily extended contact with their foster-mothers and other human caretakers. Most individuals had access to forest vegetation at some stage during their time at the station.

Human Orientation Index. To capture any psychological variation caused by time in captivity and human-related experiences, we assessed the degree to which each individual reacted toward a novel human. The Human Orientation Index (HOI) contained the following components: reactions and proximity to a human stranger during two conditions. Each subject was tested individually, except for a few cases where the mother was tested with its dependent offspring to avoid inducing stress for both. In the zoos the test took place either in the home enclosure or in the sleeping quarters if individuals were more easily separated there. In the rehabilitation stations, individuals were either transported to single compartments for testing or were directly tested in their home enclosure. The test was performed by a local man, unknown to the orang-utans and dressed in black.

The total test lasted for one minute and was composed of two consecutive conditions, each lasting 30 seconds. In the first condition the man approached and positioned himself approximately one meter in front of the enclosure where the subject was located and remained standing with his body oriented laterally (perpendicularly) to the subject. In the second condition the man turned around to face the orang-utan and tried to establish eye contact. The whole test was video recorded and during the entire test no other human was present.

Reactions and proximity to the man for the first two seconds of first sight were coded from the videos. For each condition we scored the proximity to the man in the following way: 0 = the orang-utan positioned itself as far away as possible; 1 = the orang-utan was more than one meter away from the human; 2 = the orang-utan was within one meter from the human; and 3 = the orang-utan placed itself as close to the human as possible.

We also scored the very first behavioural reaction of the orang-utan for each condition as follows: 0 = a negative reaction, defined as: retreat, stress vocalization, pilo-erection, nervous swinging or turning away from the human; 1 = a neutral reaction, defined as resting, moving calmly or play behaviour; 2 = a positive reaction, if the orang-utan approached the human; and 3 = an actively positive reaction, if the orang-utan begged (either by using lips or hands), tried in any other active way to contact the human or attempted to trade objects from the enclosure for food.

Furthermore, since the measurements listed above were based upon the first reaction of each condition only, we also scored whether any active contact behaviour occurred during the 30 seconds of each condition. This was to ensure catching the possible substantial interest in humans, when the surprise had waned.

Thus, in total HOI consisted of all the summed behavioural reactions combined with the proximity to a human stranger, with the eventual score ranging from zero to 14. In our sample, scores ranged from 2 to 14. Furthermore, we also measured the time in seconds a subject spent within one meter of the human stranger throughout the whole test and found that this independent time measurement of proximity was strongly correlated with the HOI-index (Spearman's correlation, two-tailed: $r_s = 0.600$, $N = 96$, $P < 0.001$). Given that an individual can be in close proximity and not move throughout the time of the test, but nevertheless not show any active response behaviour, we used the summarized index of both behavioural reactions and proximity scores,

which also generated more resolution to the various responses within our sample, than simply proximity latency data would.

The logistics in one of the rehabilitation stations allowed us to use a sub-sample of 28 individuals to test for social interest in unfamiliar conspecifics. In this sub-sample we measured the time of close proximity to two other unknown orang-utans of equal sex, when these were present in a neighbouring enclosure to the subject, which allowed us to disentangle social orientation per se to that from interest in humans.

Response to novelty. We performed two separate tests to assess individual variation in novelty response. First, we examined how each subject reacted to novel food. In the zoos, the novel food was blue mash potato served with black olives on top. Zoo orang-utans receive a broad diet with many types of human food, but blue items are not common and olives were new to all individuals. In the rehabilitation stations we used purple rice or purple mash potato with dried purple sweet potato pieces. Second, we introduced a novel toy in the form of a wooden board equipped with six differently coloured, rotatable tennis balls. For both tasks, we recorded the latency from task begin (when set up was completed and individual was in max. 1 m distance to the apparatus) until first touch, as well as exploration duration of the novel toy. Maximum test duration was two minutes for both tasks, and each subject was tested individually.

Experimental cognitive task – The honey tool-task. In order to evaluate cognitive performance we used a naturalistic task, which required no pre-training trials and could therefore easily be applied to all individuals. The honey tool-task allowed us to assess physical cognition of tool-use at multiple levels from very basic understanding of the apparatus and tools to high innovativeness. The task involved a wooden box measuring 50 cm × 80 cm × 5 cm, whose front was covered by a transparent Plexiglas® or Macrolon® plate (Fig. 2). The upper part of the box contained a straight channel (30 cm × 5 cm) where a wooden stick (40 cm) with its tip dipped in honey had been inserted. Below the straight channel, the box had a L-shaped channel (15 cm × 10 cm) with its bottom part filled with honey. The honey was visible to the subjects through the glass, but both channels were too long to reach the honey with their fingers. Moreover, the wooden stick could not be used to reach the honey in the L-shaped channel. In addition, below the test apparatus we provided each subject with two more wooden sticks and three pieces of rope. The ropes were too short to reach the end of the straight channel but long enough to retrieve the honey at the bottom of the L-shaped channel.

We measured multiple aspects of the orang-utans' responses to the apparatus, which was presented to them in the absence of any humans. To estimate cognitive ability, we measured the following actions: 1) removing the pre-inserted stick from the straight channel; 2) inserting any of the three available sticks into the straight channel during total test time; 3) tool manufacturing, defined as an attempt to modify the provided tools and/ or the use of any other item found by the subjects as a tool for the honey channels; 4) inserting the rope tool into the L-shaped channel. We coded each action separately as yes or no, depending on whether or not a subject performed it (Fig. 2).

We also recorded detailed data on any exploration actions during the problem-solving task. These were divided into two main categories: relevant and irrelevant. Relevant exploration concerned the channels, and thus the actual problem to be solved. Any other explorative acts directed toward the test apparatus itself, the board or table was coded as irrelevant exploration. For both categories of exploration, we measured the frequency, the duration, and the variety (see Supplementary Table S3 for definitions).

Experimental procedure. In all tasks (novelty response tests, the HOI test and the honey tool-task), only those individuals participated who could easily be separated without showing any signs of separation-induced stress. Accordingly, sample size across the different tests varied from 94 to 103. In the honey tool-task each orang-utan was tested individually, except for two mothers who were tested with their dependent offspring, in which case the offspring did not participate in the task. All subjects were naïve to this test apparatus and we performed no training trials. All subjects were tested only once. Zoo individuals were tested in their smaller sleeping enclosures where they could be separated from the group. Testing in the rehabilitation stations took place in the home enclosures, since most individuals were housed alone. For the 28 socially housed individuals, additional testing enclosures were available. The individuals were brought to the testing enclosures separately and only stayed there for the time of testing. We therefore incorporated the identity of the rehabilitation station as one factor in our analyses. The problem-solving task lasted a maximum of 10 minutes. Because the individuals' experience with humans was so variable, we conducted the problem-solving task without the presence of an experimenter to avoid possible effects on the subject's participation and attention during cognitive testing (cf. ref. 58). The task was video recorded with one to two SONY HDR-CX200 handy cameras, depending on angle of the cameras. None of the orang-utans were food-deprived for the task. In the rehabilitation stations, the honey tool-task was presented to the subjects on a large board right outside of their enclosure, and subjects could easily reach out toward the problem-solving task. In all but one zoo, the apparatus was also presented outside the enclosure. However due to the logistics and narrower mesh size in the zoos, we presented the apparatus closer to the mesh with a slight angle but less accessible to the orang-utans compared to the rehabilitation station setting. In one zoo, we presented the honey box within the test enclosure, with orang-utans having full access to the apparatus. We therefore incorporated accessibility of the test apparatus as one factor in our analyses.

Data extraction and statistical analyses. All videos were imported into Mangold interact 9.7, in which all detailed behaviours of both cognitive performance measurements as well as exploration acts were coded by SF and LD. We used IBM SPSS Statistics 20 to perform inter-observer reliability tests on every behavioural measure that occurred during the honey-tool task. For the zoo sample, 20% of the videos were coded by both observers

and yielded a Cohen's Kappa of 0.842 ($N_{events} = 1020$, $P < 0.001$), which is considered very good. From the rehabilitation sample, 16% of the videos were coded by both observers and yielded a good inter-rater agreement (Cohen's Kappa: 0.721, $N_{events} = 1020$, $P < 0.001$). Also the behavioural responses and the proximity measurements that generated the Human Orientation Index was coded in Mangold interact 9.7 by SF and a trained research assistant AS and reached a good inter-observer reliability value of 0.853 (Cohen's Kappa: $N_{responses} = 52$, $P < 0.001$). LD and SF reached an inter-observer reliability value (IOR) of 0.782 (Cohen's Kappa: $N_{responses} = 66$, $P < 0.001$) in a sample of over 26.6% of the zoo-videos. LD and and AS reached a substantial agreement within the sample of rehabilitation orang-utans of 0.701 (Cohen's Kappa: $N_{responses} = 185$, $P < 0.001$).

Further statistical analyses were performed in R version 3.2.3[59,60] using the 'lme4'[61] and 'MUMIn'[62] packages. Individual scores on each of the four measures of cognitive performance (exhibit: Yes/No) were modeled by a binomial Generalized Linear Mixed Model (GLMM). We incorporated each individual's HOI-score, age, sex, species, accessibility of apparatus, and ontogenetic background (rearing and housing condition), along with the measure of cognitive performance (Table 1) as fixed factors, and controlled for repeated observations on each individual within its respective facility by specifying this as a nested random effect. For categorical predictor variables with more than two levels, we manually specified planned contrasts. For accessibility of the test apparatus and the measure of cognitive performance (both ordinal predictor variables), we conducted polynomial trend analyses, while for ontogenetic background we set orthogonal contrasts to compare: 1) wild subjects against all other subjects, 2) subjects from rehabilitation centres against zoo subjects, 3) within rehabilitation centres, subjects from unknown provenance against all other subjects, 4) within rehabilitation centres, human-reared subjects against centre-reared subjects, and finally 5) within zoos, hand-reared subjects against mother-reared subjects. To examine each individual's relationship between the HOI scores, novelty response, exploration variables and performance, we used Linear-Mixed-Effect-Models (Figs 2, 3 and 4).

Ethical statement. All experiments fully complied with the ethical guidelines of each study facility (zoological garden/ rehabilitation station) and were respectively approved by the research manager and/or head of each facility. We confirm that according to the Swiss Animal Welfare legislation our animal experiments are considered with the severity grade 0 (no harm). The experimental protocols for the rehabilitation stations were approved by the Animal Welfare office of the University of Zurich, the Scientific Advisory Board of the BOS Foundation (Bornean Orangutan Survival), the research managers and head of the stations of Sumatran Orangutan Conservation Programme (SOCP) and Orangutan Foundation International (OFI), and the Indonesian Ministry of Research and Technology (RISTEK). Moreover, all zoo experiments were supported by research committee of the British and Irish association for zoos and aquariums, BIAZA.

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Acknowledgements

We would like to thank all the collaborating zoos and rehabilitation stations, where we conducted the study: Zoo Dortmund, Twycross Zoo, Durrell Wildlife Trust, Allwetterzoo Münster, Zoo Basel, Apenheul Primate Park, Wolfgang Köhler Primate Center at Leipzig Zoo, Blackpool Zoo and Paignton Zoo, Nyarung Menteng (BOS), Orangutan Care Center and Quarantine (OCCQ), Sumatran Orangutan Conservation Program (SOCP) – Quarantine Batu M'Belin and Danau Alo Release site. We thank Andreas Wendl for assisting the data collection

in the rehabilitation stations and Anna Schöpfer for helping out with the video coding of the Indonesian sample. In particular, we would like to thank all the station managers, animal caretakers, veterinarians and persons involved in the study at each facility, especially: Ilona Schappert, Charlotte McDonald, Gordon Hunt, Simone Schehka, Adrian Baumeyer, Thomas Bionda, Laura Salanki, Matthew Webb, Johannes Grossmann, Sebastian Schütte, Raik Pieszek, Hanna Petschauer, Ian Singleton, Yenny Saraswati, Matthew Nowak, Peter Pratje, Simon Husson and Denny Kurniawean. Additional we gratefully thank our Indonesian counterpart Universitas Nasional (UNAS), especially Drs Tatang Mitra Setia and Sri Suci Utami Atmoko and Indonesian institutions, such as the State Ministry of Research and Technology (RISTEK) and MAWAS, for their collaboration and work permissions. Finally, we would like to address our gratitude to the Swiss National Science Foundation and following foundations who have financially supported this project: A. H. Schultz Foundation, Paul Schiller Foundation and the Claraz Foundation in Switzerland and Waldemar von Frenckells Foundation, Ella and Georgh Ehrnrooths Foundation, Otto A. Malms Donationsfond, Nordenskiöld Samfundet and Oskar Öflunds Foundation in Finland. At last we would like to thank our two anonymous reviewers for their insightful and useful feedback of our manuscript.

Author Contributions

S.F. conducted the study in the European zoos. L.D. and Z.K. conducted the study in Indonesian rehabilitation stations. S.F. and L.D. wrote the paper together. E.W. performed statistical analyses. J.B., K.L. and D.H. contributed to the project planning and the experimental design of the study. J.C. and B.G. hosted the study within their research facilities. C.V. supervised the project.

Additional Information

Supplementary information accompanies this paper at http://www.nature.com/srep

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Damerius, L. A. *et al.* Orientation toward humans predicts cognitive performance in orang-utans. *Sci. Rep.* **7**, 40052; doi: 10.1038/srep40052 (2017).

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